FEEDING EXPERIMENTS AND SOME ASPECTS OF THE BIOLOGY OF THE SAND SHRIMP, CRANGON SEPTEMSPINOSA, IN LONG POND, NEWFOUNDLAND

NICOS A. HADJISTEPHANOU

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FEEDING EXPERIMENTS AND SOME ASPECTS OF THE BIOLOGY OF THE SAND SHRIMP, *CRANGON SEPTEMSPINOSA*, IN LONG POND, NEWFOUNDLAND.

by

Nicos A. Hadjistephanou ©

A Thesis

submitted in partial fulfilment
of the requirements for the degree of
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TABLE OF CONTENTS

ABSTRACT

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Laboratory experiments were conducted to investigate the effect of fresh or frozen foods of marine origin on the growth and survival of the sand shrimp, *Crangon septemspinosa*, under constant temperature conditions. The diets tested were blue mussel, squid, caplin, and TetraMin, alone and in combination.

Shrimp grew best on mussel and mussel combined diets and, less well on squid and its combinations with fish and TetraMin. The poorest growth was observed with TetraMin and its combination with fish. Moulting intervals, overall growth rates, and the survival of the sand shrimp, were all correlated with the diets.

Amino acid analyses showed the closest similarity between mussel and the shrimp; TetraMin had the least similarities, and squid and caplin were intermediate. Thus, differences in the growth and survival could be attributed to the amino acid content of the diets.

Substrate particle size and colour selection experiments showed that *Crangon septemspinosa* prefer sand to burrow in, and reject substrate with particles bigger than 2 mm. The sand shrimp selected brown substrates and avoided the white ones.

In Long Pond, Newfoundland, a size difference was apparent between males and females. Juveniles were collected in almost all the collections and were most numerous in August. Egg-carrying females appeared from April to August.

The first egg-carriers were large females; in July smaller shrimp were carrying eggs. Egg-carrying females were not collected in September and are presumed to have moved into deeper waters.

The mode of appearance of the populations segments suggests an extended breeding season. Egg-carrying females exist for 11-12 months, migrating into deeper water with the progress of the egg development. Migration of the bigger animals takes place with the cooling of the waters and inshore migration, with the increase of the temperature.

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ACKNOWLEDGEMENTS.

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To my wife, who should graduate with a degree in tolerance and understanding as a result of this experience, I extend my love and appreciation. I also extend my thanks to the whole Greek Community of St. John's for their friendship and love with which they surrounded us.

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LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

I. INTRODUCTION

I. INTRODUCTION

Of all the crustaceans suitable for sea farming, shrimps are the most important and are extensively farmed. In many tropical countries, especially those bordering the Indo-Pacific region, shrimp and prawn farming has been pursued for a long time. In the United States, where the penaeid shrimps form the most valuable commercial fishery of crustaceans, interest has developed in the possibilities of shrimp farming since the early sixties (Allen 1963). In England, studies on methods of cultivation of prawns started at about the same time (Reeve 1969).

It is believed that if shrimp culture is to succeed commercially, it must be practiced on an intensive basis. A prerequisite of such a culture is a suitable diet. This belief prompted studies on diets for the shrimp. In Japan a mixture of trash fish, shrimps and clams is fed to prawns in ponds (Hudinaga 1969) and recently the development of compounded diets is under investigation (Shigueno 1975). In England biologists also investigated the composition of freshly-prepared foods and compounded diets (Forster 1970; Forster and Beard 1969; Reeve 1969). In these studies the *Crangonidae* were almost ignored even when Regnault (1970) noticed that *Crangon septemspinosa* presents an undeniable interest for culture because of its abbreviated juvenile development.

Before 1962 *C. septemspinosa* had received little attention in contrast to numerous studies on related species

of commercial importance, especially the European *Crangon vulgaris*. Although not highly valued commercially, its role in the estuarine trophic spectrum has been recognized (Daiber 1959; Shuster 1959; Price 1962), and its growing importance has promoted studies on feeding (Welsh 1970; Wilcox 1972; Wilcox and Jeffries 1974) and growth (Regnault 1970, 1971, 1972; Wilcox and Jeffries 1973). In addition, physiological aspects of tolerance of the sand shrimp to environmental factors have been studied (Haefner 1969a, 1969b, 1970, 1971, 1973, 1976) and descriptions of various aspects of its life history throughout most of its geographic range have been made: Delaware Bay (Price 1962), Maine (Haefner 1972, Embich 1973), Newfoundland (Squires 1965), Rhode Island (Wilcox 1972).

The objective of this study was to determine if *Crangon septemspinosa* would grow equally well when fed single and combined diets of fresh or frozen foods of marine origin. The specific objective was to test the effect of diets of blue mussel, squid and fish, as well as TetraMin, alone and in combination on the growth and survival of the sand shrimp, under constant temperature conditions.

A second objective was to study the selection of substrates by the sand shrimp. Verwey (1948), in an excellent paper, approached the subject of the habitat selection of marine animals in various ways and Williams (1955a, 1955b, 1958) discussed the influence of cover in estuarine distribution. From their work it appears that the nature of the

substrate may have an important influence on the distribution of the animals which are closely associated with the bottom. Many observations confirm that various species are often found on certain types of bottom. However, mobile animals may search widely for food or cover and be in a way independent of bottom type at other times, especially during migrations. Knowledge of these relationships is limited. It is unknown whether distribution may largely be influenced by the nature of the substrate without dependency of the food supply or whether favored habitats are those with food regardless of substrate composition. In this connection, as *Crangon septemspinosa* is an unspecialized feeder, the possibility of the species attraction to bottom type is of interest.

In view of the cited evidence, and other published observations, the laboratory experiments were designed to test the following null hypothesis: adult *C. septemspinosa* are not attracted to particular bottom types, as regards to the particle size and colour, when these substrates lack food. If this hypothesis was confirmed, substrates - particle size and colour - would be considered to have little or no influence on shrimp distribution. If the hypothesis was rejected, some other influence, obviously substrates could be causing departures from the expected distribution.

Ancillary to the main onjectives, *Crangon septemspinosa* was studied in the field to obtain an understanding of some aspects of the shrimp's basic biology in Newfoundland.

Studies in the field included:

1) A years study of a population and changes in its composition. During this study the various stages of egg development were photographed.

2) Determination of the length-weight relationship.

II. LITERATURE REVIEW OF THE SAND SHRIMP

The Biology of *Crangon septemspinosa*

A. Systematics

Order DECAPODA

Suborder NATANTIA

Superfamily *CRAGONOIDA*

Family *CRAGONOIDAE*

Genus *Crago* Lamark

Crago septemspinosus Say 1818

Crangon septemspinosa Rathbun, 1904 and 1929.

Within the genus *Crangon* there are two common species: the American *Crangon septemspinosa* Say (synonymous *Crago septemspinosa)* known as the sand shrimp; and the European *Crangon crangon* Linnaeus, 1758 (synonymous *Crangon vulgaris*), known as the common shrimp. Less common species are: *Crangon affinis* from the northwest Pacific (Kosaka 1970); *Crangon alaskensis* from Alaska (Rathbun 1904); *Crangon allmani* from the eastern boreal region of the Atlantic (Allen 1960); *Crangon armillatus* from the Carribean (Hess 1941); *Crangon franciscorum* and *Crangon nigricauda* from California waters (Israel 1936). However, the taxonomic status of these less common species is not certain (Tiews 1968).

There are still some aspects of the biology of the sand shrimp which are not well known. These aspects were taken from the literature on the European common shrimp which is closely related to the sand shrimp.

B. Distribution

The geographic and bathymetric distribution of *Crangon septemspinosa* is well known. The species is boreal and sub-boreal (Gosner, 1971). It is distributed from the Arctic coast of Alaska southward along the eastern shore of Bering sea to the Shumagins and on the east coast of North America from eastern Florida (Say) northward (Rathbun 1922) to the Gulf of St. Lawrence and northeastern Newfoundland (Squires, 1965). It is a littoral estuarine decapod normally found in shallow waters, however, Rathbun (1922) states that it was found in depths of about 800 m off Delaware and Whiteley (1948) collected the animal in 450 m.

C. Life history

Egg development is related to the water temperature. The eggs of *Crangon septemspinosa* hatch into the larva which is the first zoeal stage, since the nauplius stage is passed in the egg. The larval stages of the sand shrimp were described by Needler (1941) and Tesmer and Broad (1964). Subsequent moultings take the zoea through the 2nd to the 6th stage where it is called the postlarval stage. Tesmer and Broad noted that metamorphosis to postlarva took 13-19 days after hatching at 18-20°C.

Lebour (1931) listed the general characters of larvae of *Crangonidae*. There seems to be a close similarity between the larvae of *C. septemspinosa* and *C. vulgaris*; according to Needler (1941) minor differences occur in the first and fifth stages of development, and growth, as

C. vulgaris grows faster than the sand shrimp. Otherwise, the larvae of the two species are "remarkably alike."

Depending on the season in which they were hatched, the shrimp mature in 3 to 12 months at about 25 mm in total length. The females outnumber the males and the percentage of females is highest during the spawning period. Females can live more than three years and males more than two years, attaining body lengths of up to 70 mm and 47 mm respectively (Price, 1962).

The major breeding season of the sand shrimp is from March to October (Price, 1962). Haefner (1972, 1976) suggests that some females carry eggs during most of the year, and that ovigerous females are the most numerous from January through June.

D. Conditions for life

Crangon septemspinosa is commonly known as the sand shrimp, because it is an epifaunal member of sand communities (Wilcox 1972). However, observations on this point vary. In Newfoundland the species is found in many - but not all - sandy areas around the coast, particularly those with eel-grass (*Zostera*) (Squires 1965); Whiteley (1948) says that it may occur in all kinds of bottom. Wilcox and Jeffries (1973) describe the substrate of the collection areas as fine to coarse sand. Haefner (1973) collected the animals from an area characterized by fine sand over mud and clay. Rathbun (1922) found the shrimp on sandy mud with stones. Ackman and Hooper (1973) collected

it from a sandy bottom and Creaser (1973) refers to it as the mud shrimp.

Crangon septemspinosa is a member of the benthic communities. During daylight hours the animals are generally buried in the substrate; food or mechanical disturbance are enough stimuli to cause the shrimp to emerge from the substratum (Wilcox, 1972).

The sand shrimp is a good example of an estuarine inhabitant. Within the estuarine zone its population encounter wide ranges of salinity and temperature. Haefner (1969b, 1971) reports that it has been collected within temperature and salinity ranges of (-3) to 25°C and 3.4 to 32 ‰ respectively, and is able to detect and avoid anoxic conditions.

Haefner (1969b) showed that *Crangon septemspinosa* is an osmoregulator. It demonstrates hypoosmotic regulation in normal seawater (30-35 ‰) and low temperatures of 5°C and, hyperosmotic regulation in diluted seawater (3-25 ‰) and warmer temperatures of 15°C. The former conditions are encountered during the winter months in deeper, cooler and more saline waters offshore and the latter, during the summer in shallower, warmer and mesohaline waters inshore. Although the osmoregulatory pattern of the sand shrimp seems unusual, it can be related to the animal's biology and migratory behaviour within the estuarine zone.

Haefner (1969a, 1969b, 1970) also showed the interraction of environmental temperature, salinity and

oxygen levels on the survivorship of the shrimp. The species is susceptible to low oxygen tensions, with the female shrimp and especially the egg-carrying ones being more sensitive than the males. At normal levels of dissolved oxygen in seawater (10-12 mg/liter), males demonstrated 100% survival at salinity ranges of 19-36 ‰ and temperature ranges of 10-14°C; females demonstrated 100% survival at the same temperature ranges but slightly bigger range of salinity 18-39 ‰. Mortality was always observed when low oxygen concentrations (2-3 mg/liter) were combined with ranges of temperature 5-24° and salinity 5-45 ‰. The salinity-temperature tolerance of the shrimp under low oxygen conditions as compared to normal oxygen conditions was shifted towards lower temperatures and higher salinities.

E. Migrations

The sand shrimp undergo vertical migration (Welsh 1970) and onshore - offshore seasonal migration (Haefner 1969a, 1969b, 1972). The onset of darkness stimulates vertical migration with a significantly increased swimming activity. Welsh (1970) demonstrated that, although the presence of prey *Neomysis americana* and *Artemia salina* is largely responsible for prolonging their activity and determining the distribution of the shrimp in darkness, *Crangon* is little affected by their presence during daylight.

Older (larger) shrimp undergo seasonal migration to deeper waters in the fall and to shallower waters in the spring, probably in response to prevailing water temperatures

and the interaction of temperature, salinity and oxygen levels. "Thus, in the fall when temperature of the shallow waters of the estuary drops below 5-7°C and mortality becomes significant, the movement into deeper and more saline regions has survival value, providing that other conditions for life are satisfactory. Migration towards the shore of the shallow and warmer estuarine waters of 10-14°C in the spring are initiated because these waters are better suited to the shrimp's needs than deeper, cooler, waters." (Haefner 1969a, 1969b, 1970, 1971, 1972, 1976).

F. Predation

Wilcox (1972) reports that predation is probably the dominant factor limiting the abundance of the species. Adult shrimp are prominent in the diets of numerous carnivores such as weakfish, skates, and stripped bass (Price 1962; Creaser 1973). The larvae are very susceptible to cannibalism from adults and heavy predation from ctenophores.

G. Growth

Regnault (1970) observed the growth of *C. septemspinosa* at a constant temperature of 20°C in the laboratory from metamorphosis to sexual maturity. He estimated the growth rate from size increments and moult frequencies, using the classic Hiatt growth diagram, and made the following observation:-

1) The salinity has no appreciable effect on the growth rate except in mass culture.

2) The composition of the diet has only a slight influence on the growth rate if *Artemia* are included. In contrast, the final size and the moult frequency are determined by the quantity of available food. However, even in a semi-starvation condition, the slopes of the growth rates are constant.
3) Growth in mass culture is slower than the growth in isolation.
4) The development of the external sexual characteristic and sexual maturity are determined more by the size than the age of the shrimp.

Price (1962), using length-frequency distributions of shrimp from field populations, estimated the growth rate of *C. septemspinosa* to be 0.4 mm/week and free from seasonal variation.

Wilcox and Jeffries (1973) showed that the growth of the sand shrimp is a function of water temperature and initial size. According to them, growth is greatest during the summer and, conversely, lowest in cooler waters. An inverse relationship between growth rate and size was shown, i.e. larger shrimp have a lower growth rate than smaller. Their growth equations describe a family of lines since smaller shrimp of both sexes grow faster than larger ones at the same temperature.

Female *Crangon crangon* have a greater growth rate (Meixner 1968, 1969); female *Crangon* sp. attain larger sizes (Price 1962; Meixner 1968, 1969); and female *Crangon septemspinosa* have greater life expectancy than males (Price 1962).

According to Wilcox (1972) and Wilcox and Jeffries (1973) 20-30 mm shrimp moulted twice a month at 20°C and grew 3-5 mm over two intermoult periods in the laboratory. This rate agreed with their field data, but was several times greater than Price observed.

Meixner (1968) made the following observations regarding growth and moulting of *Crangon crangon* reared in the laboratory:-

1) Growth rates appeared to be directly related to the quantity of food available and to water temperature, while growth rates were inversely related to body size.
2) Regeneration of amputated limbs retarded growth.
3) Adult females grew less per moult than males but moulted more often.
4) A maximum increase in length per moult was 6.5 mm for females in the 30-40 mm size range.
5) The interval between two successive moults was directly influenced by the quantity of food and the water temperature and inversely related to body size.
6) There were three distinct phases of growth in a moulting period:
   a) no size change in the first three days after moult;
   b) a continuous though relatively small growth (less than 1 mm in 13 days of the intermoult period);
   c) a rapid growth upon moulting.

H. Feeding

Individual *Crangon* have diverse feeding habits. *Crangon vulgaris* were judged by Lloyd and Yonge (1947) as an omnivore after algae, polychaetes, gastropods, bivalves, amphipods, fish eggs and larvae were found in their stomachs. However, they suggested that the common shrimp prefer animal tissue. Tiews (1968), reviewing the literature on *C. vulgaris*, judged it to be omnivorous, but animal tissues were the main food items. *Crangon allmani* was classified by Allen (1960) as a carnivore, but he noted that sand and mud were always found in the digestive tract. *Crangon affinis* was classified by Kosaka (1970) as a carnivore, although sand and mud were always present with the food.

Crangon septemspinosa was classified by Price (1962) as a secondary consumer, i.e. one trophic level was between it and primary producers. A variety of planktonic and benthic invertebrates, crustacea being the predominant item, where found in the gastric mills, which generally were similar to those listed for *C. vulgaris* and *C. allmani*. Price suggested that the sand shrimp may derive benefit secondarily from detritus emitted from salt marshes by consuming filter feeders (mysids and small bivalves) which were feeding on decaying detritus and its associated bacteria. He also suggested that scavenging probably contributes to the high incidence of organic debris in the stomachs of *C. septemspinosa*.

Wilcox (1972) showed that the sand shrimp is an

unspecialized feeder. In laboratory experiments he demonstrated that *C. septemspinosa* will ingest a variety of organic matter and that they are able to derive nutrition from all the foods ingested, although some foods were more nutritious than others. However he felt that this behaviour cannot be confirmed in nature, because of the limitations of the methodology and the ability of the shrimp to rapidly and efficiently triturate their food. Wilcox's experiments will be described in the discussion.

Regnault (1970) fed juvenile *C. septemspinosa* with diets of *Artemia* nauplii alone, *Artemia* nauplii + eggs of *Arbacia*, and *Artemia* nauplii + algae (*Monochrysis* and *Cyclotella*). He found similar growth and survival and suggested the important role of glycosides and proteins on growth.

III. MATERIALS AND METHODS

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A. Collecting area

The shrimp for both field observations and laboratory work were collected from the head of the west part of Long Pond, Newfoundland (Figure 1).

The area was partly described by Christie (1967). A small river empties into the Pond, which is adjacent to the sea. The bottom is characterized by sand and mud on which are beds of blue mussells (*Mytilus edulis*), and patches of eel grass (*Zostera marina*) are present all over the area. A characteristic sample of substrate of the collecting area was analysed and classified as sandy silt. (Figure 2).

The area sampled was about 400 m along the shore. Maximum depth of capture was 1.5 m. At the beginning of every collection, the water temperature was measured, as well as salinity and conductivity. Measurements were taken from about 20 cm beneath the surface and from the bottom at the depth of 1.5 m. Samples from the same depths were taken for pH analyses.

B. Field studies

1. Length-frequency distribution and population structure.

Crangon septemspinosa was sampled over a period of one year in the field. Collections were made parallel to the shore with a hand net of 50 x 25 cm opening (2 mm mesh).

About 850 shrimp were collected for the purpose of field studies. Collections were planned to be in regular monthly intervals, but, during the winter months, this was

Figure 1: Long Pond

(The arrow indicates the area from where a substrate sample was analyzed).

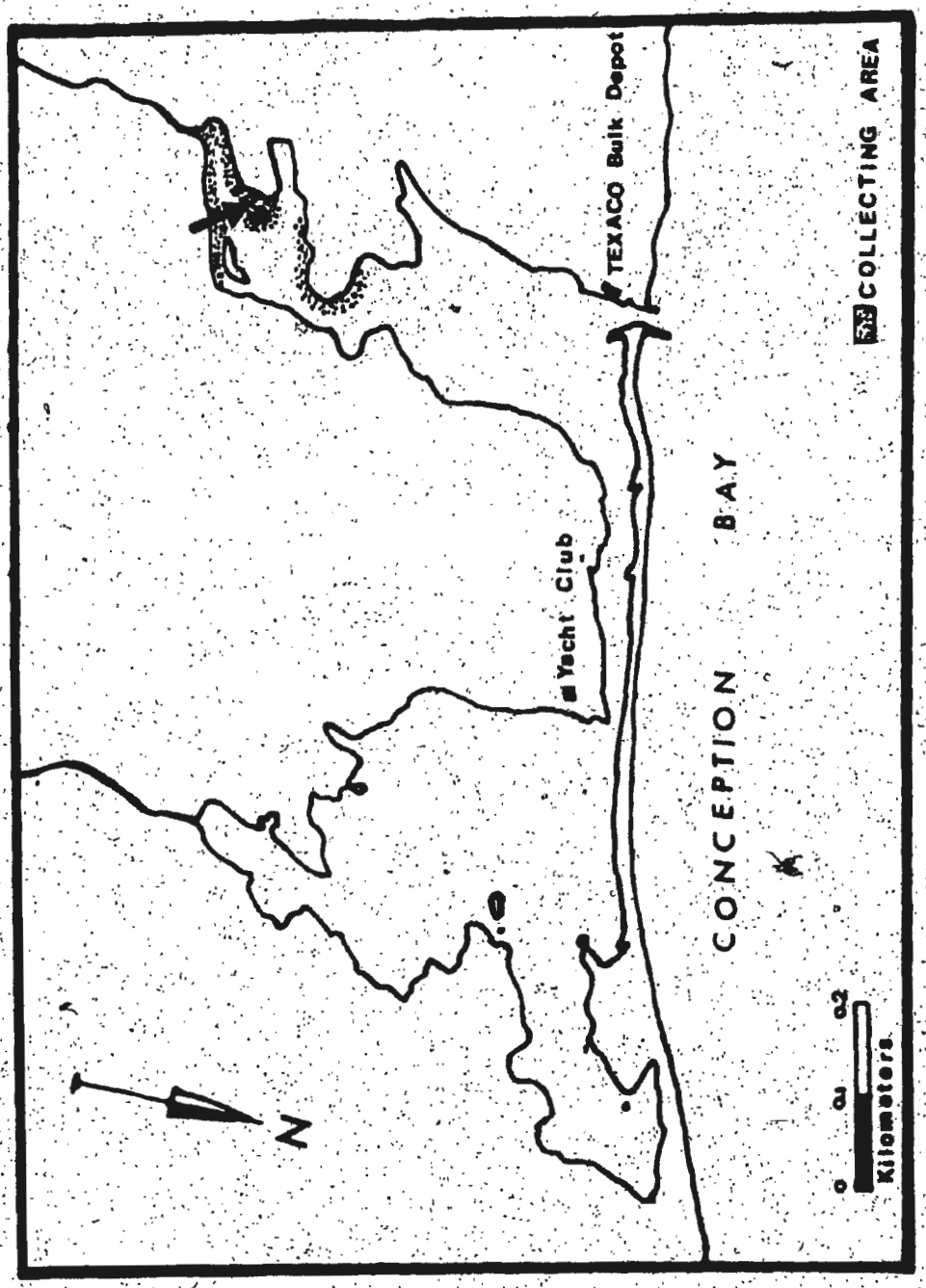
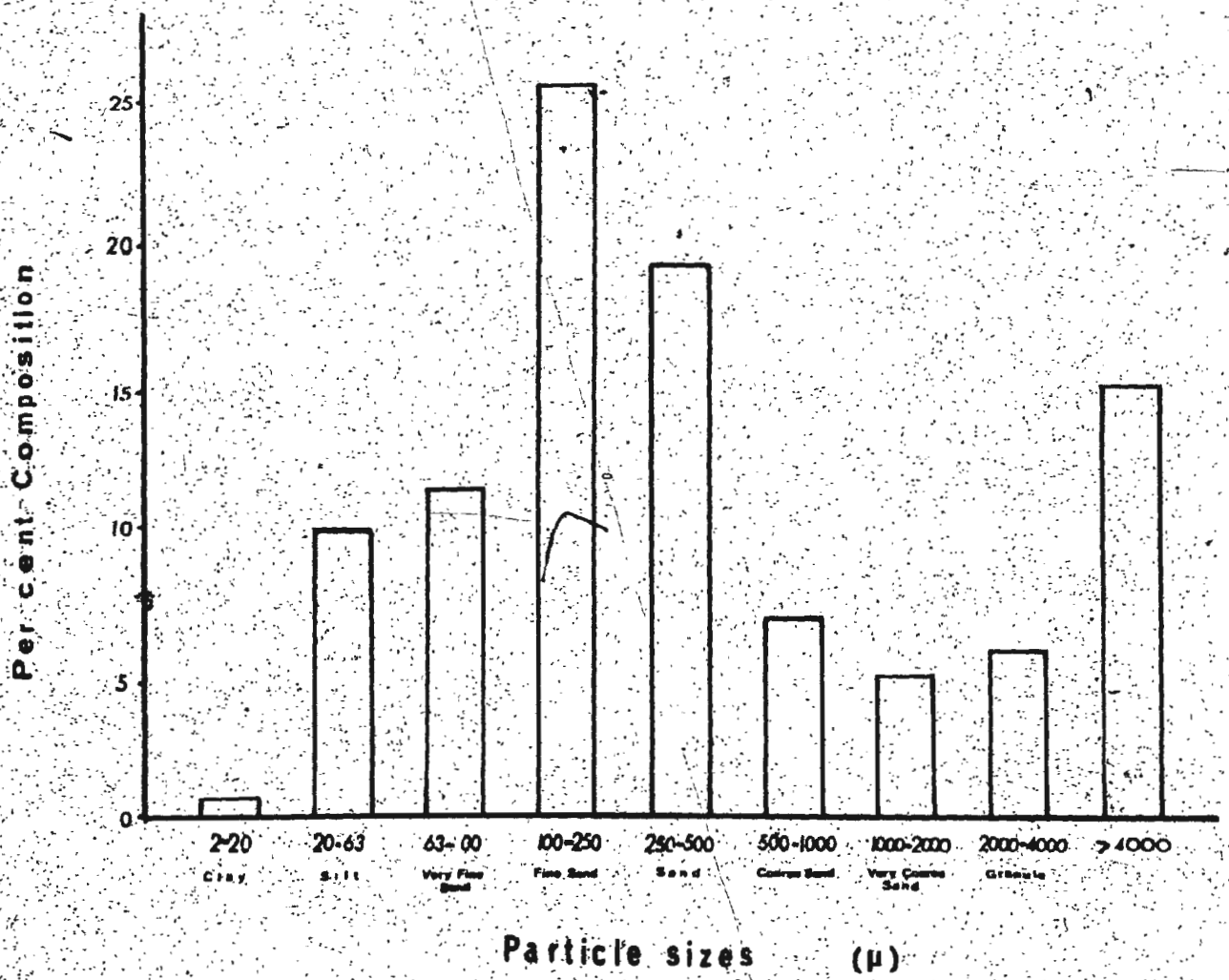

TEXACO Bulk Depot
COLLECTING AREA
Yacht Club
CONCEPTION BAY
N
0
1
2
Kilometers

Figure 2

Per cent particle-size composition of a representative sample of the substrate at the area where shrimps were collected in Long Pond.


Per cent Composition
25
20
15
10
5
0
2-20
Clay
20-63
Silt
63-00
Very Fine Sand
100-250
Fine Sand
250-500
Sand
500-1000
Coarse Sand
1000-2000
Very Coarse Sand
2000-4000
Granule
>4000
Particle sizes (μ)

not possible, because the area was sometimes ice covered; as a result, the collections during the winter were made at irregular intervals.

In collections containing less than one hundred shrimp, all were measured and classified, otherwise 100 shrimp were collected from the field for this purpose. Measurements for total length were made according to Price (1962). The shrimp were sexed according to the description of Meredith (1952) for *Crangon vulgaris*. The sex of specimens less than 20 mm long was impossible to determine and are referred to here as juveniles. All females were examined for the presence of an egg mass attached to the abdomen; such females were classified as "egg-carrying females." This term was preferred as being more descriptive than "ovigerous", "berried", and "egg bearing."

In order to correlate the observed size per category of animals with the temperature each month, data were transferred to punch cards for a computer analysis according to multiple regression of SPSS package. (Statistical Package of Social Sciences).

2. Length-weight relationship.

Length-weight relationships were determined for male, female, egg-carrying female and juvenile shrimp. For wet-weight determinations, shrimp were rolled on paper towels to absorb excess water adhering to appendages and egg pad and weighed to the nearest 0.01 g on a Mettler top-loading balance. For dry-weight, the shrimp were dried in an

oven at 100°C for 24 hours and weighed on an Oertling balance to the nearest 0.1 mg. Data were transferred to punch cards for regression analysis, which was made with the computer program FRB SA040 QQCV4 (Simple regression).

3. Egg development

Eggs from egg-carrying females were taken and examined with a microscope to determine their stage of development. Photographs were taken, in order to illustrate the various stages of egg development.

C. Substrate - Selection Experiments

1. Preliminary Observations

Preliminary observations included:

a. The congregation of the shrimp

Observations of the shrimp in a rectangular tank showed that they may congregate in its corners. Because similar observations made elsewhere (Forster, 1970), showed that prawns kept in large tanks tend to cluster along the sides and the corners of the tanks, it was concluded that, in order not to bias the results, the rectangular tank should be avoided.

To overcome this bias, a wooden decagonal tank was constructed. This was the closest to the circular construction which could conveniently be made of wood. The diameter of the tank was 80 cm and its height was 20 cm. On each side a 1 cm diam. hole was drilled, 1 cm from the top. The tank was divided by 35x1x3 cm boards into 10 triangular compartments. All the boards were joined to a 10 cm diam. central wooden

core, and in this way the compartments were equilateral triangles of 35 cm sides and 25 cm bases. The whole construction was coated with non toxic layers of fiber glass and approximately 3 cm of substrate was put in each compartment. The experimental tank is shown in Plate 1.

b. Burrowing behaviour

For detailed observations of the burrowing methods and behaviour, individual shrimp were placed in containers and allowed to burrow. The containers were filled with about 10 cm of substrate. Vertical views of animals in the substrate were obtained by using plexiglass containers measuring about 25 cm; width was restricted to about 3 cm with pieces of glass which were fitted in the containers.

c. Distribution experiments

Experiments were made in the decagonal tank to determine the special distribution of the shrimp. Coarse sand was put in all the divisions of the tank and 20 shrimp were put in it. Observations were made for 12 days. In the first five days the shrimp were put at the beginning of the daily observations in such a way to make sure that two shrimp were burrowed in each division. In the next seven days the shrimp were released in the middle of the tank.

Results from each method of releasing the shrimp were summed together and subjected to a chi-square test of the null hypothesis that the shrimp were randomly distributed in all sections of the tank.

2. Particle-size selection

The substrate was collected locally and was subjected to standard methods of mechanical analysis, particles larger than 0.063 mm being graded with sieves and, smaller sizes by the method of Krumbein and Pettijohn (1938). The substrate, mixed sand, was sorted into 10 categories of particle size according to a modification of Wentworth's classification of soil particle grades, shown in Table 1.

TABLE 1

Approximate particle size and classification of the 10 substrates used in the particle-size selection experiment

CLASSIFICATION	PARTICLE SIZE mm
Pebble	>4
Coarse Granule	3 - 4
Fine Granule	2 - 3
Very Coarse Sand	1 - 2
Coarse Sand	0.500 - 1.000
Sand	0.250 - 0.500
Fine Sand	0.100 - 0.250
Very Fine Sand	0.063 - 0.100
Silt	0.020 - 0.063
Clay	0.002 - 0.020

The experiment was designed to allow animals a free choice among these 10 substrate types, under uniform conditions. To do this, the substrates, all of the same colour, were burned to 600°C for 24 hours to assure absence of food; they were then placed randomly in the compartments of the decagonal tank.

To avoid any phototropic orientation of the animals, the tank was covered during the experiment. Running sea-water was introduced in the middle of the tank and it flowed out by the holes drilled on the sides of it (Plate 2).

The experiment consisted of 3 replications. Each replication consisted of 10 observations over a ten-day period. New animals were used in each replication. A total of 20 shrimp were assumed to be the maximum tolerance without crowding. The shrimp used were adults of the same carapace length of 7 mm (40-45 mm total length). Equal numbers of males and females were used. Fresh substrates were used at each new replications, except in a few instances when some materials were used for two successive replications.

Counts were made in the morning. Welsh (1970) found that *C. septemspinosa* were significantly more active at night and activity tends to decrease thereafter. In order to count the shrimp, the tank was uncovered and a diaphragm (Plate 3) was immediately inserted to block the shrimp in the compartments (Plate 4). Thus, even if the shrimp emerged from the substrate, it was impossible to escape to another part of the tank. Usually the animals were not very disturbed. The shrimps were collected, placed in another

PLATE 1: The experimental tank for the substrate selection.

PLATE 2: The experimental tank covered.

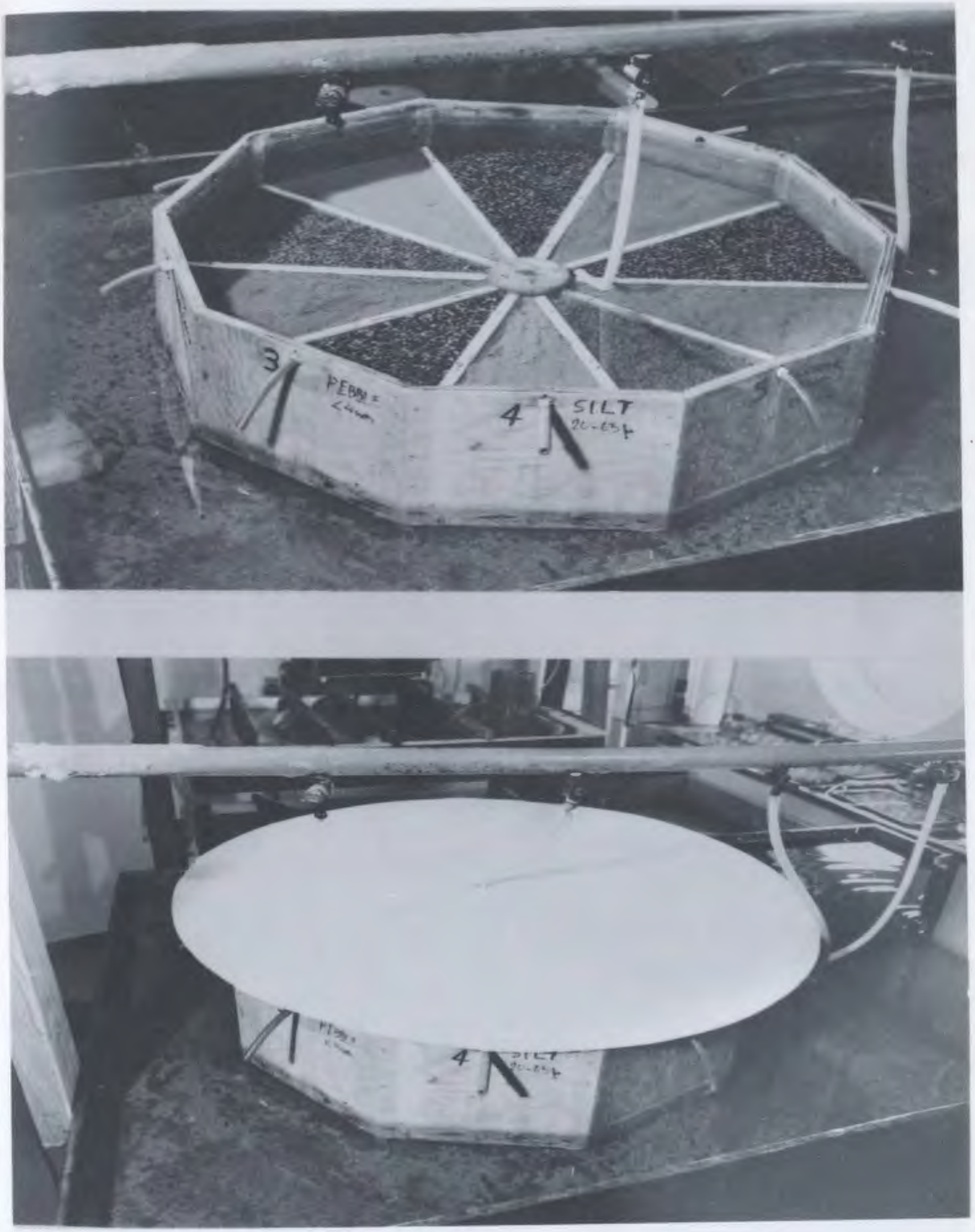
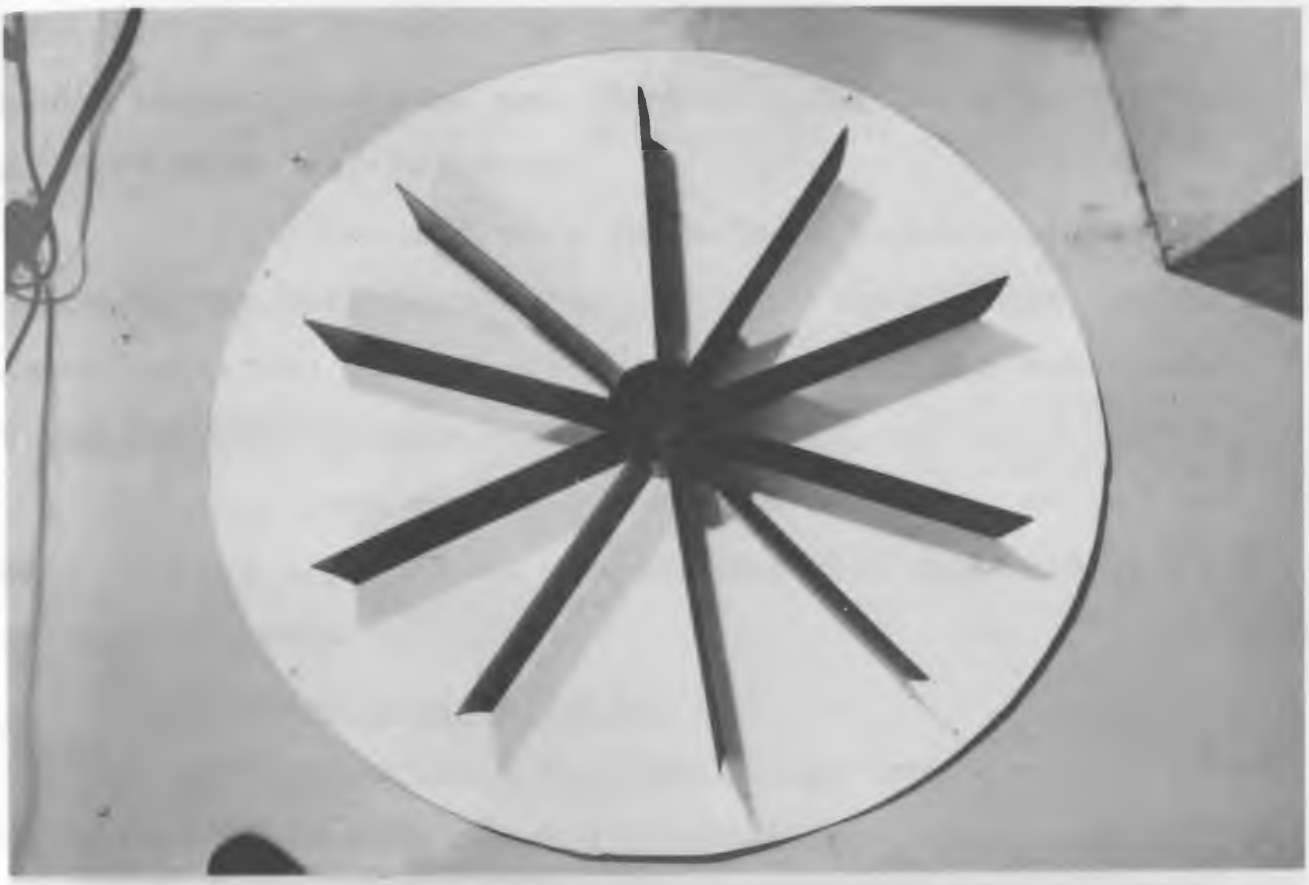

3
PEBBL
<4mm
4
SILT
20-63μ

PLATE 3: The diaphragm used to block the shrimp in the compartments of the tank.

PLATE 4: The diaphragm in the tank when shrimp were counted.




4
SILT

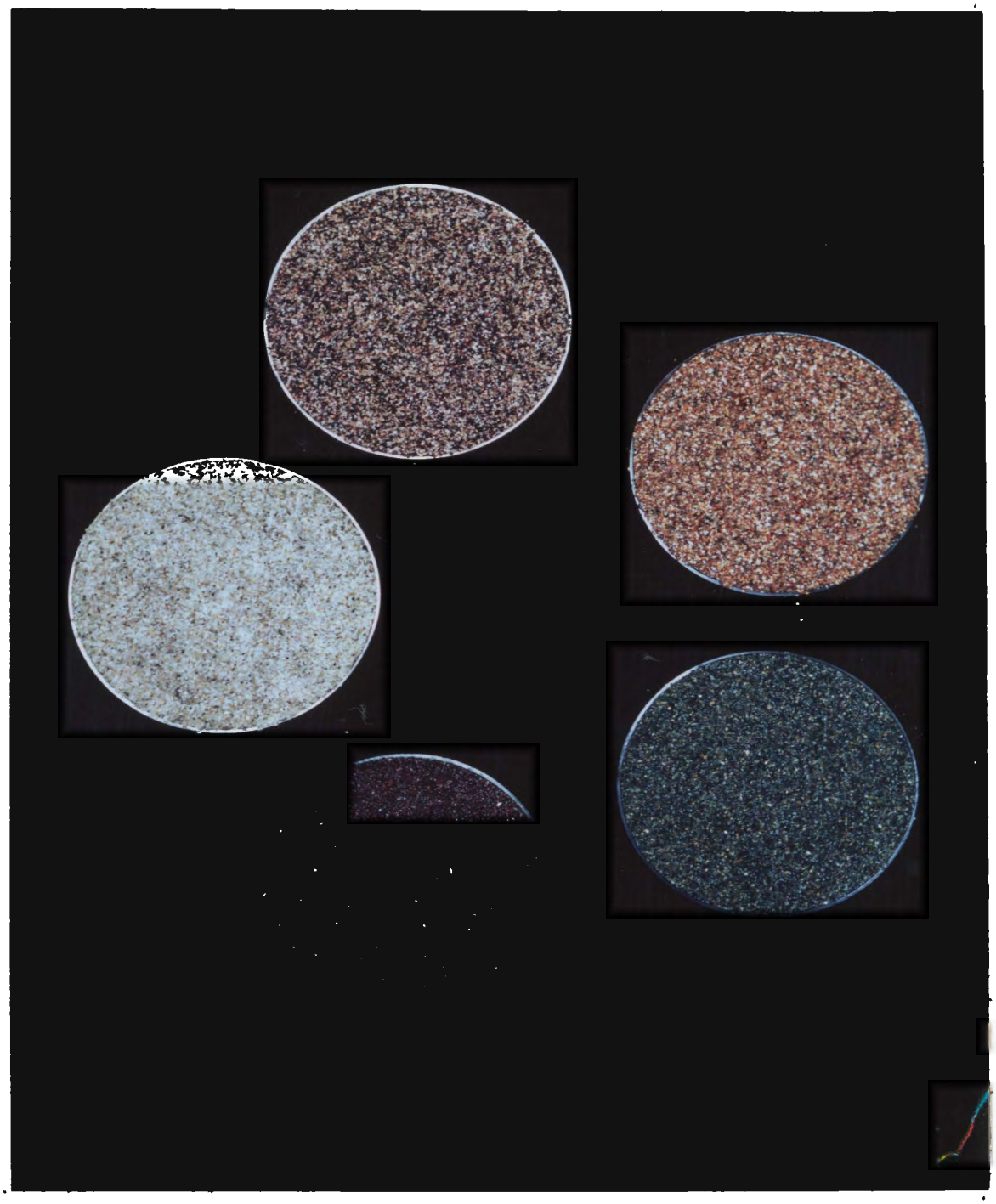


PLATE 5: The colours used in the colour-selection experiment.

container, and released in the middle of the tank 2 to 4 hours later. The tank was covered again and a gentle flow of the water was adjusted.

Temperatures were taken by a Temperature-Salinity-Conductivity meter after the count of the shrimps, as well as Salinity and Conductivity. A sample of the water was taken and pH was measured.

Any cast exoskeletons were removed. At the end of each ten-day replication the shrimps were examined for stomach fullness.

3. Particle-colour selection

The experiment was run in the same decagonal tank as the particle-size selection experiment. The same procedure was followed and the same measurements were taken.

In five of the compartments a different substrate colour was put, alternating empty compartments with compartments containing substrate. The colours used were all natural, collected locally; they are shown in Plate 5. All the substrates were of the same particle-size of 0.250 - 0.500 mm (sand).

The tank was not covered and in each replication its position was changed.

In such free-choice situations, if no attraction of the particle size and the colour was exhibited, shrimp would be expected to have frequented the different compartments randomly after many observations. Thus, they were counted for a total of 30 days in each experiment (3 sepa-

rate replications).

Results from the 30 day counts of shrimp of each experiment were summed together and subjected to a chi-square test of the null hypothesis that adult *Crangon septemspinosa* are not attracted to substrates of particular particle sizes or colours when these substrates lack food.

D. Feeding Experiments

1. Experimental animals

All the animals used in the experiments were collected from Long Pond in May and August, 1977, and were transported to the laboratory in plastic buckets. The journey from the Pond to the laboratory lasted about one hour. Shrimp which were transported in this way survived well and almost no mortalities occurred. When arriving in the laboratory the shrimp were put in tanks with running sea water of about 13°C which was the temperature of the collection area. They were then sexed according to the dimorphism of the first and second pleopods described by Meredith (1952) for *Crangon vulgaris*, and left overnight with an absence of food. Only shrimp that could be sexed were included in the experiment and this avoided the difference in growth rates observed by Regnault (1970) between juveniles and preadults.

2. Experimental vessels

The feeding experiments were made with shrimps kept individually. This avoids the problems of cannibalism, especially in the starved animals (Welsh, 1970) and permits observations on each shrimp individually, as of mortality,

moulting, etc. To do this, individual cages were made of fly screen, measuring 8.5 x 8.5 x 14 cm (Plate 6). The cages were put in plexi-glass or polystyrene tanks approximately 28 x 38 x 18 cm. In each tank twelve shrimp were placed and were fed the same diet (Plate 7). Air was bubbled in the tanks and 2-3 cm of sand substrate was put in. All the tanks were covered with plastic fly-screen.

No attempt was made to regulate the photoperiod.

3. Seawater

The experiment was made with the use of running sea water. The water was warmed to 13°C in a thermostatically controlled container. The central pipe was then divided into branches in the tanks and the water flowed out the tanks into a channel, so that they were practically placed in a water bath of approximately the same temperature as the warmed water (Plate 8).

4. Food supply and preparation

The food supplied were fresh blue-mussel (*Mytilus edulis*), frozen squid (*Ilex illecebrosus*), caplin (*Mallotus villosus*), and TetraMin (commercial fish flakes of the Tetra Werke Co. of W. Germany) and their combinations, shown in Table 2. The shrimp were fed to excess every 24 hours; food remaining after this time was removed before fresh food was added. Considerable attention was given in the removal of excess food and the cages were well cleaned before fresh food was placed in them. At irregular intervals the sand from the tanks was changed because of the danger of the

PLATE 6: The cage where shrimp were put individually, and the dimensions.

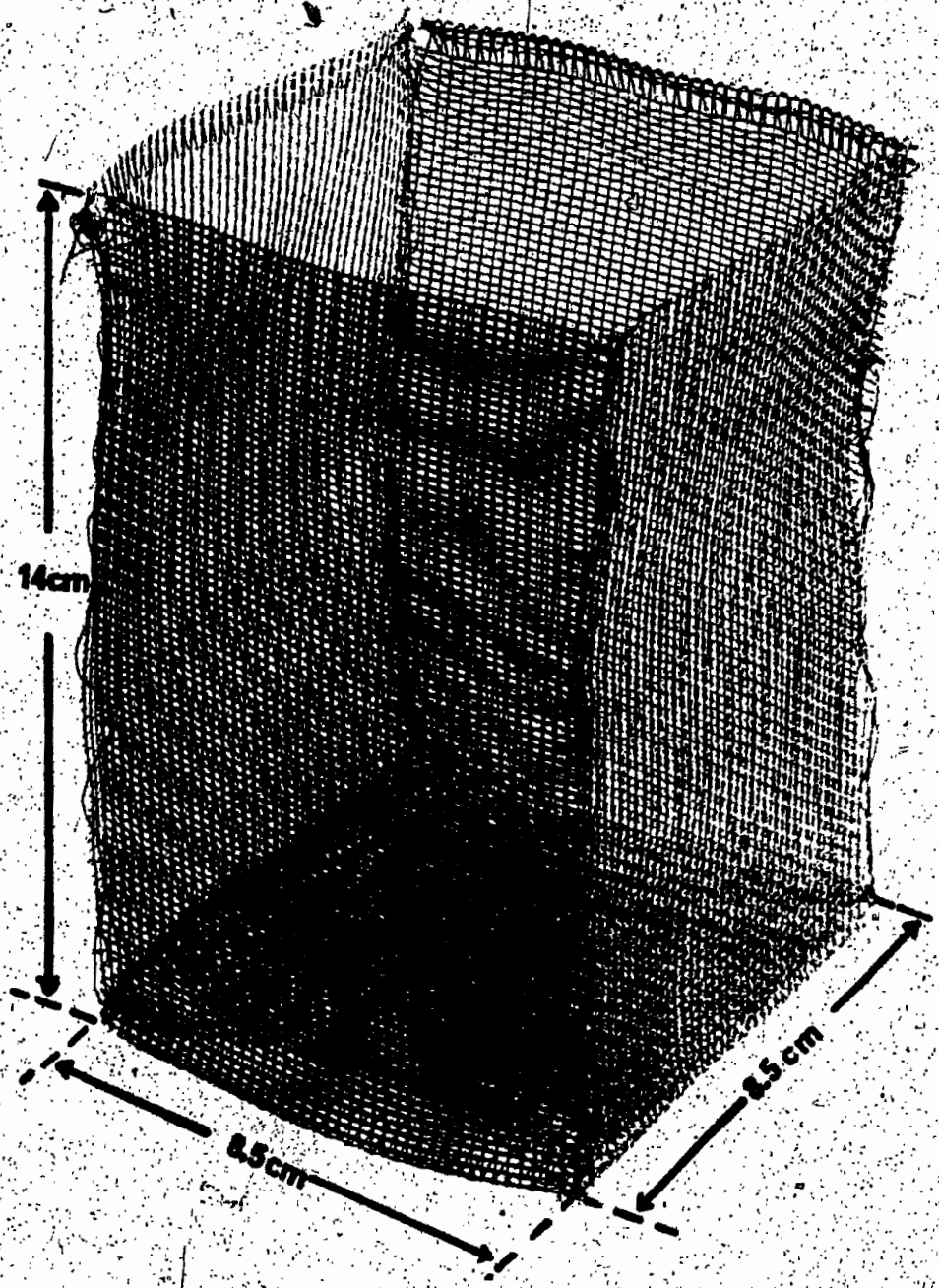

14cm
8.5cm
8.5cm

PLATE 7: The experimental tanks with the cages in them.

PLATE 8: The whole set-up of the feeding experiment.

TABLE 2

The diets used in the first feeding experiment, with the abbreviations which are used in the text.

Squid	
Mussel	
Caplin	
TetraMin	(T. min)
Squid + Mussel	(S + M)
Squid + Caplin	(S + C)
Squid + TetraMin	(S + T)
Mussel + Caplin	(M + C)
Mussel + TetraMin	(M + T)
Caplin + TetraMin	(C + T)
Squid + Mussel + Caplin	(S + M + C)
Squid + Mussel + TetraMin	(S + M + T)
Squid + Caplin + TetraMin	(S + C + T)
Mussel + Caplin + TetraMin	(M + C + T)
Squid + Mussel + Caplin + TetraMin	(S + M + C + T)
Starved	

matter becoming anaerobic especially in the lots fed TetraMin and its combinations.

The foods were prepared in the following ways. Mussels were opened, the meat removed from the shells and chopped into small pieces; the squid and caplin were defrozen overnight; TetraMin was mixed with water and stirred so as to form a paste. Combinations of foods were put in petri dishes and stirred well so that the particles would be mixed as much as possible and the shrimp would not be able to separate them. These foods will subsequently be called diets.

Mussels, squid and caplin were collected locally. The mussels were gathered in large numbers and kept alive in storage tanks with running seawater in the laboratory until they were required. Squid and caplin were cleaned of the viscera and minced with a hand mincer when fresh. Both were put in small plastic bags and were deep-frozen. Every night a bag of each was defrozen to be used the next day as food.

The shrimp were fed every day except every 14th day when they were weighed. In this case the cages were cleaned the previous day and the animals were fed the next day, immediately after they were weighed. This procedure was followed (a) to allow the animals to digest their food so that they all would be weighed with empty stomachs and (b) not to disturb them too much by cleaning the cages and then weighing them.

Observations of the shrimp during the experiment

showed that they fed freely on all the diets and they were frequently seen to have food in their stomachs. All diets evoked feeding responses, even diets in which this was not expected, such as TetraMin.

5. Weighing of live animals

In the experiments an estimated growth rate was required. This was estimated, among other ways, in terms of increase of live weight per unit time.

Every 14 days the shrimps were removed from their cages, put into individual glass containers with sea water and brought to a top loading balance. They were then gently dried on sheets of tissue paper and weighed to the nearest 0.01 gram, after which they were returned to the glass containers and, finally, to their tanks. Newly - moulted shrimp were weighed the next day so to allow time for the soft cuticle to start hardening.

6. Measurement of total length

In the experiment it was desirable to measure the length and the length increment of shrimps. The total length of the shrimp was measured to the nearest millimeter from the anterior end of the spine on the antennal scale to the posterior tip of telson according to Price (1962). Newly - moulted animals were measured for total length four days after moulting to determine length increments. The shrimp were also measured for total length every 14 days for a second check of their length.

7. Observations

The shrimp were numbered in the tanks and a separate record was kept for each. On the record there were noted: The date, Weight, (Total) Length, Moult date, Days between moults, and Survival of the shrimp, i.e. the days which the shrimp had survived from the beginning of the experiment. Wherever it was possible, the reason for the death was noted, e.g. "Moult failure." An example of such a record is given in Table 3.

The cages were inspected each morning for deaths and exuviae. Deaths and moults were listed on the records; the exoskeletons were easily seen and removed when the cages were being cleaned. After moulting a small number of shrimp consumed their own exuviae and some moults almost certainly went unrecorded as a result. Such an error could be easily recognized, however, by an uncharacteristic gap in the moulting pattern of the shrimp concerned and also by an unusually large increase in length between the recorded moults.

The feeding experiments were made in two phases: For the first feeding experiment 6 male and 6 female shrimp in individual cages were put in each tank and fed the same diet for 112 days. Immediately after the first experiment, a second one started of the same, 112 day - duration. The purpose of the second feeding experiment was to investigate further the results of the first one, as well as to clear some details of the first feeding experiment and to gather

TABLE 3

Representative records from the first Feeding experiment

DIET: Mussel

Shrimp No: 5

Date	Weight gm.	Molt Date	Length mm.	Days between molts
May 29	0.22		28	
June 12	0.28	June 1	34	16
June 26	0.31	June 16	37	16
July 10	0.40	July 1	40	16
July 24	0.49	July 16	42	16
Aug. 7	0.58	July 31	45	19
Aug. 21	0.69	Aug. 18	47	20
Sept. 4	0.70	Sept. 6	48	22
Sept. 18	0.78	Sept. 27	50	

DIET: Mussel + TetraMin

Shrimp: No: 5

Date	Weight gm.	Molt Date	Length mm.	Days between molts
May 29	0.53		42	
June 12	0.59	June 14	44	17
June 26	0.70	June 30	46	17
July 10	0.84	July 16	48	20
July 24	1.02	Aug. 4	53	22
Aug. 7	1.15	Aug. 25	56	25
Aug. 21	1.20	Sept. 18	58	
Sept. 4	1.24			
Sept. 19	1.30			

more data on the survival and the moulting frequency. This experiment was in all the details the same as the previous one, except that the shrimp used in it were 12 males and 12 females for each diet. Much attention was given to the initial length of the shrimp. From the 12 shrimp used in each tank, 6 were of initial length 30-40 mm, 4 of 40-50 mm and 2 of 50-55 mm, so that moulting frequency and growth would be determined in size classes.

The diets used were:

1. Squid
2. Mussel
3. Caplin
4. Squid + Mussel + Caplin, and
5. Starved

At the same time, the remaining live shrimp from the first experiment in the above diets were kept and fed with the new ones, all the observations continued, so that their survival rate could be determined in a long-term experiment.

8. Amino acid analyses

Although the objective of this study was not primarily to deal with food composition, amino acid analyses were made of the following:-

Sand shrimp,

Blue mussel,

Squid,

Caplin, and

TetraMin.

The materials were ground in a blender and the particulate matter was filtered; 10% Trichloroacetic acid was added and the materials were centrifuged at 10,000 rpm for 15 min. at 4°C. The fluid layer was removed, the tubes cooled in liquid N_2 and put in a vacuum pump. After this, the specimens were given to the Analytical Ultracentrifuge Amino acid Facility of the Department of Biochemistry for hydrolysis with 6N HCl, final preparation and quantitative analyses of the conjugated amino acids by liquid chromatography.

9. Statistics

For the analysis of the results, growth was broken down to "Increase in the length," "Increase in the weight," "Moulting frequency" and "Growth rate "; the "Survival" of the animals was also determined.

To determine the "Increase of the length" and the "Increase in the weight," the growth diagram of Hiatt was used.

Hiatt (1948), in a paper on the biology of the crab *Pachygrapsus crassipes* proposed a diagram constructed according to a method in which the pre-moult sizes on the x axis were plotted against the post-moult sizes on the y axis. The points thus plotted fell on straight lines. On the basis of this evidence he found it possible to calculate the size at each successive instar as well as the number of moults necessary to reach a particular size.

Kurata (1962) gave mathematical interpretation of Hiatt's diagram and demonstrated that the growth data

obtained from a wide variety of crustaceans, if plotted according to this method, give straight lines. He also demonstrated that this is true not only for the linear dimension, as was found by Hiatt, but also for the intermoult weight.

Kurata termed the constants in the equations as growth coefficients. He observed the presence of inflection points in the diagrams and he suggested the correlation of them with the commencement of sexual maturity. Thus, Kurata proposed that, according to the value of the growth coefficient, the growth pattern of a crustacean may be divided into three types, and adopted criteria to distinguish these types. This way, the life of the crustacean may be divided into three growth phases: the larval, the juvenile, and the mature phase; each phase is characterized by different values of the growth constants, which can be derived from the growth data. Generally, the growth coefficient for the dimensional increase is between 0.8 and 1.4 and is greater in the younger growth phase than the older one.

In his paper, Kurata could not give an adequate explanation of why the growth data, when plotted according to Hiatt's method, give a straight line, nor could he establish the biological significance of the growth constants. However, he suggests that, "if it is of empirical nature, the growth rules proposed, will be applicable without hazards to the analysis of the growth of crustaceans, and indeed are very convenient."

Regnault (1970) used this method when studying the laboratory growth of *Crangon septemspinosa* from metamorphosis to sexual maturity. To avoid the difference in growth rates observed by Regnault between juveniles and preadults, only shrimp that could be sexed were included in the present experiments, as was also done by Wilcox and Jeffries (1973). Thus, no inflection point ought to appear in the diagrams.

The data were transferred to punch cards for regression analysis according to the Hiatt growth diagram for both, increase in the weight and increase in the length; for the weight the diagram was made on a time basis. The sets of data were first compared in groups of two diets for significant differences with the computer program FRB SA040 QQCV4 (simple regression). After computing the regression equations for each diet, the lines were plotted according to Hiatt's growth diagram.

The data were then transferred to the computer program BMDOIR where comparisons for significant differences were permitted in more than two groups. Thus, the equations were compared among them in order to find the relations of growth in the various diets and, if possible, to classify the diets according to their effectiveness. For the first feeding experiment a total of 138 comparisons for each, weight and length, were made. Other comparisons were made between the male and female shrimp on the same diets and, further, comparisons were made among the common diets of the first and second feeding experiment.

The survival and the moulting frequency of the animals were obtained from the records kept for each shrimp. The growth rate was derived from the moulting frequency and the increments between moults, and it was used as an overall checking for the calculated results and the classification of the diets in groups.

The Poisson distribution was used to test whether deaths due to moult failure were random. Finally, the Mann-Whitney U-test was applied to compare the differences in survival between male and female shrimp fed the same diets.

IV. RESULTS

IV. RESULTS

A. Field Studies

Crangon septemspinosa were collected from water in which the salinity ranged from 3.0 to 28.0 ‰ and the temperature, from 0.0 to 24°C (Table 4).

1. Length-frequency distribution and Population structure.

Length-frequency distributions of 843 shrimp are shown in Figure 3. Although conditions did not permit regular and adequate collections during the winter months (December to March), shrimp were found in Lond Pond during all months of collection.

Generally *Crangon septemspinosa* were numerous from April through November, 1977. Females were larger than the males (see Tables 6 and 8). This difference is more obvious in bigger individuals. The largest male collected was 56 mm and the largest female was 77 mm - both collected in October.

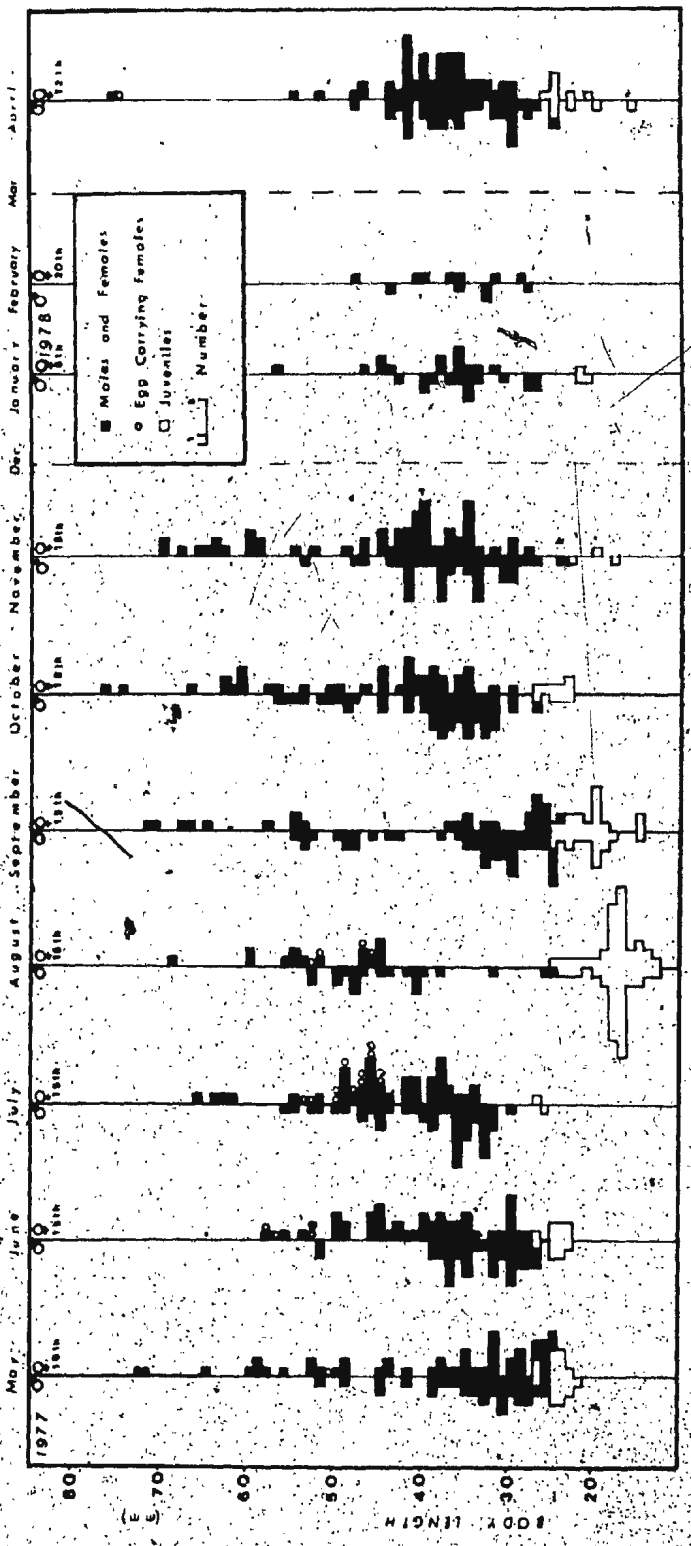
Most females were not carrying eggs. Egg-carrying females, although not so abundant, were collected from April to August. When first appearing, egg-carrying females were large shrimp, but during the following months were replaced by smaller individuals (75 mm in April, 51-73 mm in May, 45-54 mm in July and 46-53 mm in August). Although complete records were not kept, observations on the egg development show that, when they first appear in the population in April, egg-carrying females carry eggs in the first stages of development, further, during the last month of their presence in the population in August, these females carry eggs in the

Table 4: Hydrographic data associated with collections of *Crangon septemspinosa* in Long Pond, Newfoundland.

Date		Temp. °C	Salin. ‰	Cond. µMHOS	PH
May 18, 1977	Surface	15.5	4.0	450	7.25
	Bottom	13.0	27.0	28000	7.85
June 15, 1977	Surface	18.0	4.5	3000	8.90
	Bottom	20.0	25.0	35000	9.85
July 15, 1977	Surface	24.0	6.0	10000	9.50
	Bottom	20.0	28.0	37800	10.25
Aug. 15, 1977	Surface	20.5	27.5	35500	10.69
	Bottom	20.5	26.5	10000	10.67
Sept. 15, 1977	Surface	13.0	8.0	26500	9.40
	Bottom	13.0	23.5	22000	10.00
Oct. 15, 1977	Surface	12.0	8.0	24200	9.00
	Bottom	10.0	21.0	7300	9.15
Nov. 15, 1977	Surface	12.0	7.0	12500	8.55
	Bottom	11.0	11.0	205	8.75
Jan.6, 1978	Surface	0.0	11.0	18000	7.80
	Bottom	0.5	22.0	6000	8.20
Feb. 20, 1978	Surface	0.0	7.0	11000	6.80
	Bottom	0.0	12.5	480	6.80
March 15, 1978	Surface	0.0	6.0	900	6.50
	Bottom	3.0	11.0	900	6.55
April 12, 1978	Surface	6.0	3.0	2200	6.90
	Bottom	2.0	21.0	19500	7.90

Figure 3

Length frequency distribution of *Crangon septemspinosa* in Long Pond, Newfoundland, during 1977-1978.


Males and Females
Egg Carrying Females
Juveniles
Number
1978
1977
April
March
February
January
December
November
October
September
August
July
June
May
80
70
60
50
40
30
20
BODY LENGTH (mm)

middle stages of egg development.

Juveniles were collected in all samplings, except February. The most numerous and smallest juveniles, collected in August, increase in size to November; there is no apparent increase in their length from November to May. From May these animals appear in the length-frequency distributions as mature shrimp which increase in size in the next months and then most disappear. If the disappearance is due to mortality, the life span of most shrimp would be about 1½ years. Relatively few large shrimp (>70 mm) in their second year were caught.

The biggest shrimp which was not sexed was 27 mm. Since the smallest sexed male and female animals were 24 mm, there is an overlap from 24 to 27 mm of shrimp of differentiated and nondifferentiated sexual characteristics.

Within the total sample of shrimp, the ratio of males to females was almost the same (1:1.09, males:females). The sex ratio was unequal and inconsistent throughout the year:- During the months of August, September, October, males outnumbered the females 1:1.41 and during January, 1:1.15; during the months April to July, females outnumbered the males 1:1.31 and during November, 1:1.43.

The number of male, female, egg-carrying female and juvenile sand shrimp collected in Long Pond are given in Table 5 and the per cent figures are plotted in Figure 4; Figure 5 gives the actual number of shrimp.

Table 6 shows the observed size per category each month and the temperature each month in Long Pond. These

TABLE 5: Number of male, female, egg-carring female and juvenile *Crangon septemspinosa* and per cent proportions of them collected in Long Pond, Newfoundland, 1977-1978.

Date	Male		Females		Egg Carrying ♀		Juveniles		Total
	No.	%	No.	%	No.	%	No.	%	
May 18, 1977	34	34	44	44	3	3	19	19	100
June 15, 1977	38	38	45	45	4	4	13	13	100
July 15, 1977	45	45	40	40	13	13	2	2	100
Aug. 15, 1977	20	20	14	14	4	4	62	62	100
Sept. 15, 1977	45	45	25	25	-	-	30	30	100
Oct. 15, 1977	51	51	39	39	-	-	10	10	100
Nov. 15, 1977	40	40	57	57	-	-	3	3	100
Jan. 6, 1978	15	48	13	42	-	-	3	10	31
Feb. 20, 1978	5	42	7	58	-	-	-	-	12
April 12, 1978	37	37	51	51	1	1	11	11	100

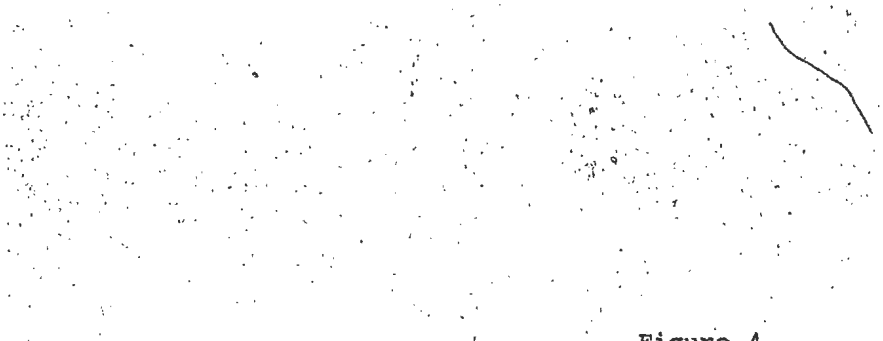


Figure 4

Percent proportions of male, female, egg-carrying female and juvenile *Crangon septemspinosa*, collected in Long Pond, Newfoundland, in 1977-1978.

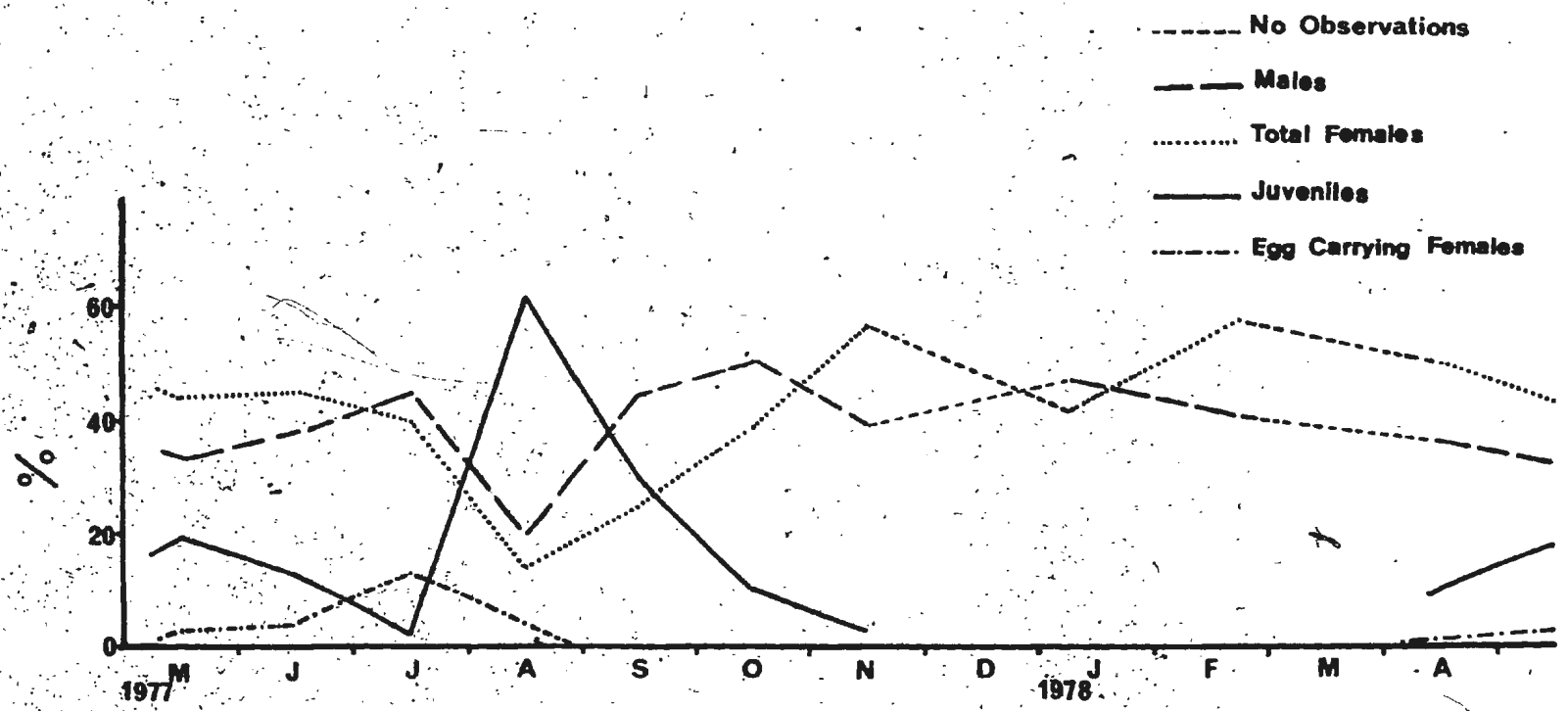

No Observations
Males
Total Females
Juveniles
Egg Carrying Females
%
60
40
20
0
1977
M
J
J
A
S
O
N
D
1978
J
F
M
A

Figure 5

Proportions of male, female, egg-carrying female and juvenile *Crangon septemspinosa* collected in Long Pond, Newfoundland, in 1977-1978.

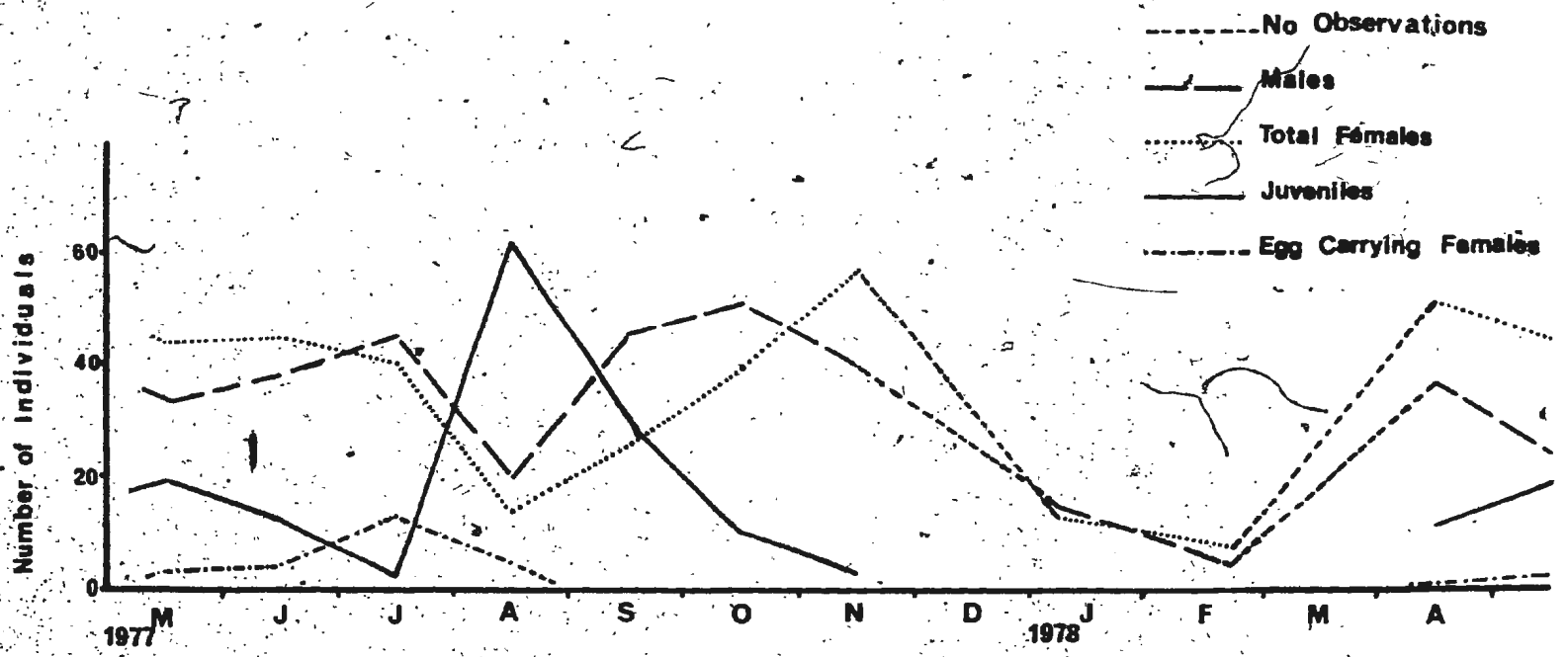

No Observations
Males
Total Females
Juveniles
Egg Carrying Females
Number of Individuals
60
40
20
0
M
J
J
A
S
O
N
D
J
F
M
A
1977
1978

TABLE 6

Observed and Expected size per category and per month of *Crangon septemspinosa* in mm and the Temperature each Month in Long Pond.

Numerical Value (X_2)	Month	Temperature (X_1) °C	MALE		FEMALE		EGG-CARRYING		JUVENILES	
			Observed	Expect.	O	E	O	E	O	E
1	April	4.0	35.73	33.25	39.67	38.51	75.00	74.50	23.09	24.28
2	May	14.0	34.03	36.01	38.93	41.67	58.92	60.70	24.56	23.88
3	June	19.0	33.08	37.55	40.31	44.55	55.25	53.36	24.58	23.49
4	July	22.0	39.40	38.59	44.65	46.53	48.23	48.62	26.50	23.09
5	August	20.5	43.05	38.54	52.57	46.50	49.50	49.70	18.02	22.69
6	September	13.0	35.47	37.01	41.60	43.78	-	58.53	20.77	22.29
7	October	11.0	38.76	36.83	47.53	43.53	-	60.26	24.70	21.89
8	November	11.5	36.55	37.26	45.30	44.39	-		20.33	21.50
	December	-	-	-	-	-	-	-	-	-
9	January	0.5	34.13	34.88	40.23	40.11	-		21.67	21.10
10	February	0.0	34.80	35.07	37.57	40.53	-		-	20.70
	March	1.5	-	35.75	-	41.84	-		-	20.30

data yeild the lines discribed by the following equations:

$$L = 0.245\ X_1 + 0.311\ X_2 + 31.958 \quad \text{for males}$$

$$L = 0.448\ X_1 + 0.641\ X_2 + 34.114 \quad \text{for females}$$

$$L = -1.294\ X_1 - 0.865\ X_2 + 80.544 \quad \text{for egg-carrying females}$$

$$L = -0.398\ X_2 + 24.679 \quad \text{for juveniles.}$$

where L is the length of the animal, X_1 is the temperature of the month and X_2 is the numerical value of the month in question, where April is 1, May 2, etc. The equations indicate that the mean length of the population increases for males and females in the warmer months and decreases in the cooler months, while for the egg-carrying females the opposite happens, i.e., their length decreases with the warming of the water and increases with the cooling of it. The length of juveniles is independent of the temperature and depends upon the numerical value of the month. The expected sizes of each category per month, calculated according to the above equations are shown in Table 6.

The equations are discriptive but can be used to predict the expected mean size of the categories of the animals in a certain month, if the water temperature is known. They also fit to the pattern of appearance of each category of shrimp in the population. For example the equation for the egg-carrying females describes the decrease in the size of these animals in the summer and the increase of their size in the cooler months. April was chosen to have the numerical value of 1, because the first

regular catch after the winter and the first egg-carrying female was collected in this month.

2. Length-weight relationship.

The regression equations computed for the wet and dry weight of *Crangon septemspinosa* are presented in Table 7. On the basis of these equations, plots of length-weight relationships are presented in Figure 6.

The female regression line is elevated higher than the regression line of male shrimp, and the egg-carrying regression line is higher in elevation than that of female animals. This was expected, because the mass of the eggs contributes to the weight of animals without affecting their length.

Table 8 presents the calculated wet weight for representative size sand shrimp and numbers per kilogram.

The regression equations, as computed in this study, are much the same as the equations calculated for the sand shrimp by Haefner (1973). Comparing Table 8 with Haefner's results it can be said that the animals appear to be slightly heavier in Chesapeake Bay than in Long Pond. This difference might be due to weighing errors, although this does not seem to be true, if the larger animals are compared, because the difference in weight increases for the heavier animals. On the other hand, the specimens of this study were taken throughout the year, while the specimens in Haefner's study were taken only during two months in spring when more food might be avail-

TABLE 7

Length-weight Relationship of *Crangon septemspinosa* in Long-Pond, Newfoundland. Sex, wet and dry weight, number of observations, the regression equations, the correlation coefficient and the ranges in size and weight.

SEX		NUMBER OF OBSERVAT. N	EQUATION	CORRELATION COEFFICIENT r	RANGES			
					LENGTH (mm)		WEIGHT (g)	
					min.	max.	min.	max.
MALE	Wet	331	log W = -5.3034796 + 3.0251798 log L.	0.984	24	56	0.09	1.03
	Dry	330	log W = -5.9093783 + 3.0175238 log L.	0.978	24	56	0.0131	0.2498
FEMALE	Wet	335	log W = -5.4943533 + 3.1636914 log L	0.991	24	77	0.09	3.16
	Dry	334	log W = -5.9755588 + 3.0752560 log L	0.981	24	77	0.0211	0.7634
EGG CARRYING FEMALE	Wet	35	log W = -5.7101718 + 3.3110325 log L	0.988	45	75	0.56	3.05
	Dry	35	log W = -5.8806829 + 3.0840407 log L	0.950	45	75	0.1620	0.7973
JUVENILE	Wet	152	log W = -5.8358781 + 3.4311208 log L	0.932	13	27	0.010	0.13
	Dry	153	log W = -5.3007160 + 2.5998461 log L	0.958	13	27	0.0040	0.0350

W = Weight in (g) and L = total Length in (mm)

Figure 6

Length-weight relationship of 331 male, 335 female and 153 juvenile *Crangon septemspinosa*. (Solid line: wet weight. Broken line: dry weight.)

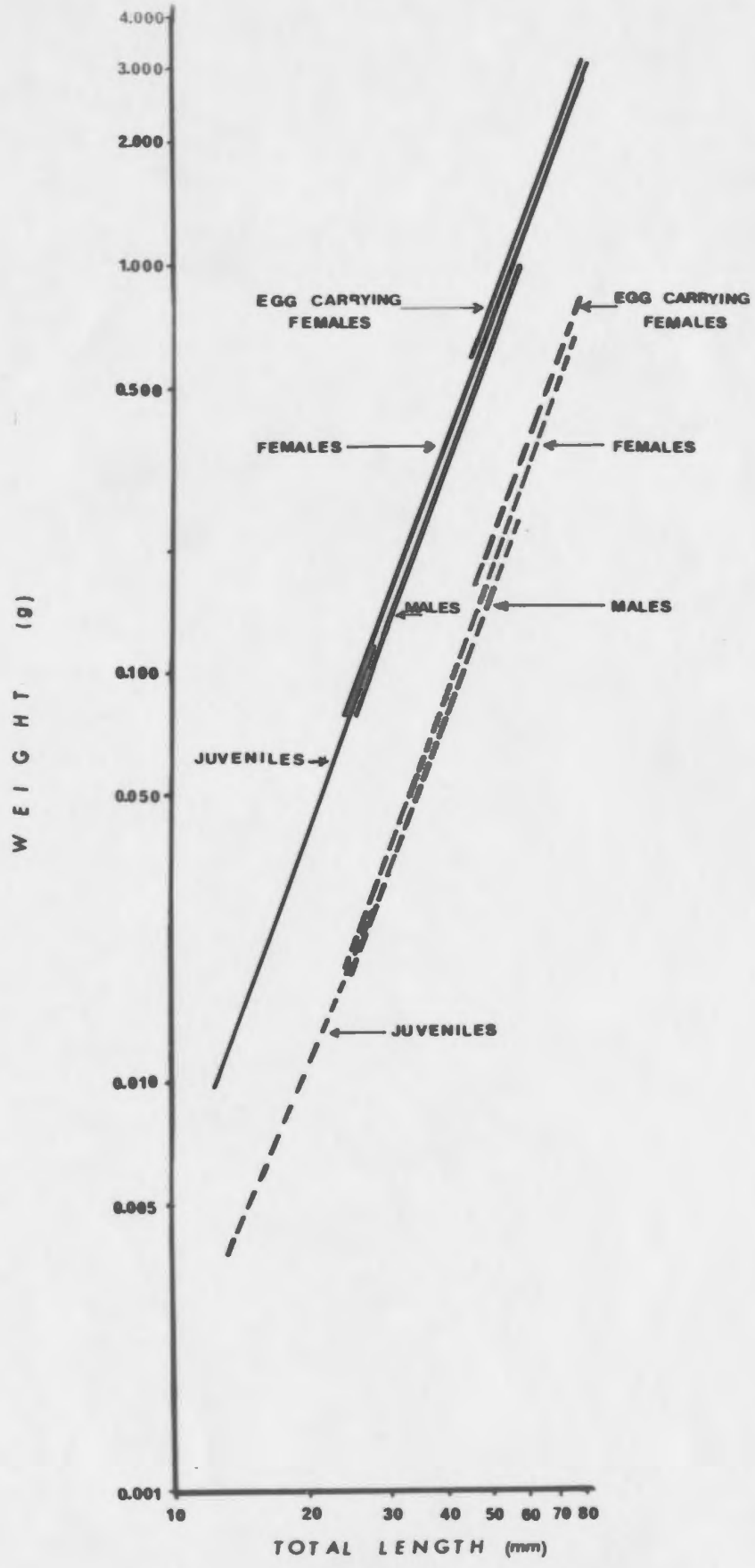

4.000
3.000
2.000
1.000
0.500
0.100
0.050
0.010
0.005
0.001
WEIGHT (g)
EGG CARRYING FEMALES
EGG CARRYING FEMALES
FEMALES
FEMALES
MALES
MALES
JUVENILES
JUVENILES
10
20
30
40
50
60
70
80
TOTAL LENGTH (mm)

TABLE 8

Calculated wet weight of representative size *Crangon septemspinosa* and extrapolated number per kilogram.

SIZE mm	MALE		FEMALE		EGG CARRYING FEMALE	
	Mean Weight (g)	No/kg	Mean Weight (g)	No/kg	Mean WEIGHT (g)	No/kg.
25	0.098	10204	0.107	9346	—	—
30	0.150	6667	0.166	6024	—	—
35	0.235	4255	0.260	3846	—	—
40	0.339	2950	0.377	2653	—	—
45	0.500	2000	0.525	1905	0.630	1587
50	0.684	1462	0.764	1309	0.846	1182
55	0.929	1076	1.037	964	1.196	836
60	—	—	1.437	696	1.630	613
65	—	—	1.741	574	—	—
70	—	—	2.330	429	—	—
75	—	—	2.933	341	2.900	345

able; this difference might have caused the small discrepancy, which otherwise is not easily explained.

3. Egg development

The stages in the development of the egg were photographed, and these photographs were used to produce the Plate 9. As the egg development is a continuous biological procedure, the stages included in this Plate only represent a few phases of it, and, consequently, are arbitrary.

The development of the egg in Plate 9 is classified in four stages which are further subdivided:

Stage A: Upper row, from left to right.
Newly-laid, spherical egg to the starting of gastrulation.

A_1: egg newly-laid, spherical, yolk uniform;
A_2: egg enlongated in one diameter;
A_3: egg bullet shaped;
A_4: gastrulation starting.

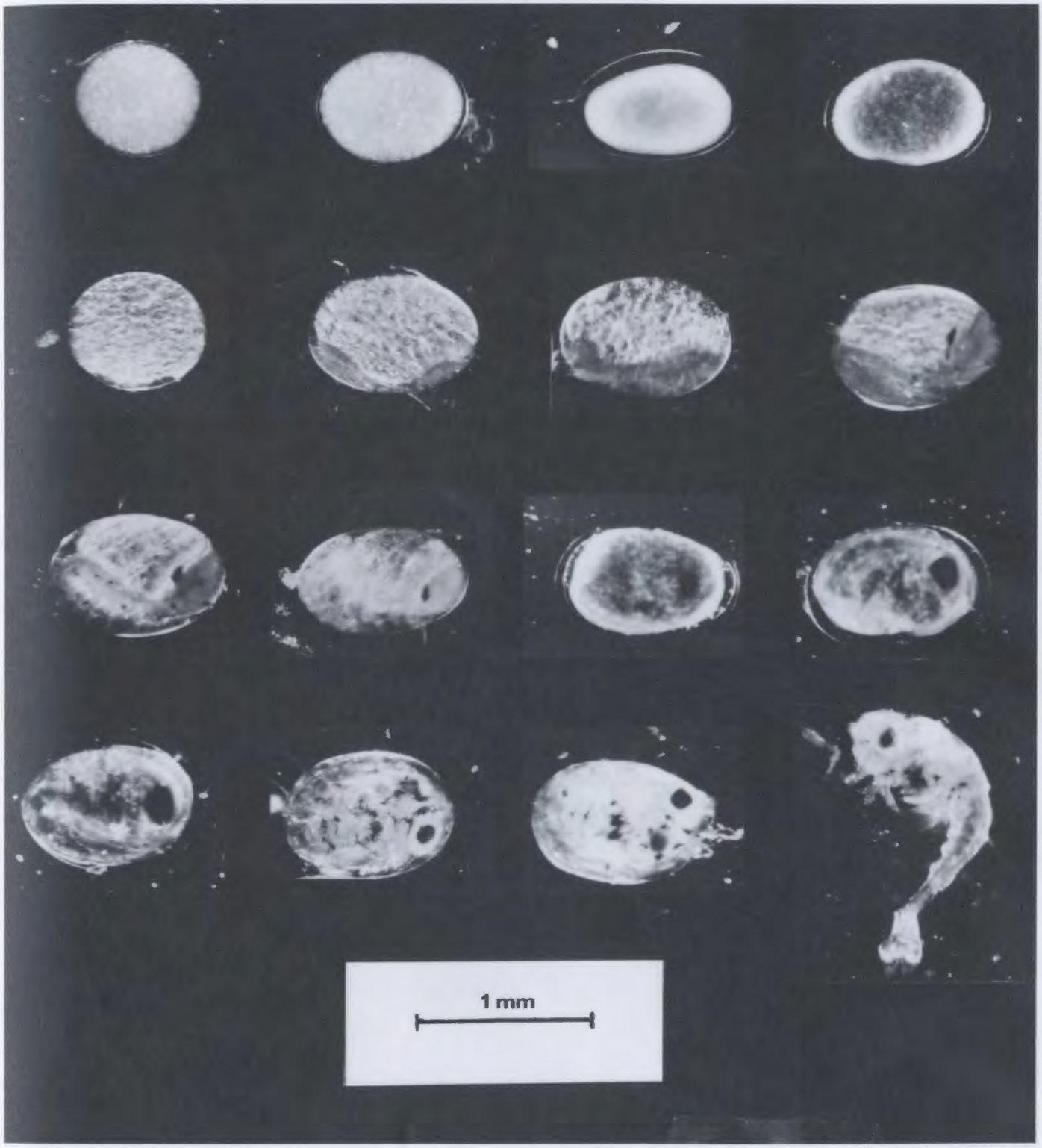
Stage B: Second row, from left to right.
Gastrulation and segmentation.

B_1: gastrulation in progress;
B_2: early segmentation of the body;
B_3: final segmentation before the appearance of the eye;
B_4: visible eye.

Stage C: Third row, from left to right.
Eye enlarging to carapace and abdomen full size.

C_1: eye larger;
C_2: outline of carapace and abdomen visible;

PLATE 9: Stages in the development of the egg of the sand shrimp, *Crangon septemspinosa*.


1 mm

C_3: abdomen increased in length;

C_4: eye almost full size, carapace and abdomen full size but not separate.

Stage D: Last row, from left to right.

Eye full size, abdomen free from head, no yolk visible and hatching.

D_1: eye full size, abdomen free from head, no yolk;

D_2: pre-larval stage, larva full size confined in the egg;

D_3: larva hatching.

A zoea, just hatched is shown at lower right.

These stages are similar to those described by Price (1962) and used by Embich (1973) for *C. septemspinosa*, and by Meredith (1952) and Lloyd and Yonge (1947) for *C. vulgaris*.

The egg development is directly related to water temperature with hatching occurring in about 3 weeks at 20°C according to Wilcox (1972). Lloyd and Yonge (1947) report that for *C. vulgaris* the duration of the egg-carrying intermoult is approximately 5 weeks at 12°C. In the laboratory the first egg-carrying females, observed at the middle of January, were still carrying eggs of stage C_1 at the end of June, i.e. after about 20 weeks, at a maximum temperature of 8°C in June and minimum 2°C in January.

B. Substrate-selection Experiment.

1. Preliminary Observations.

a. Burrowing behaviour.

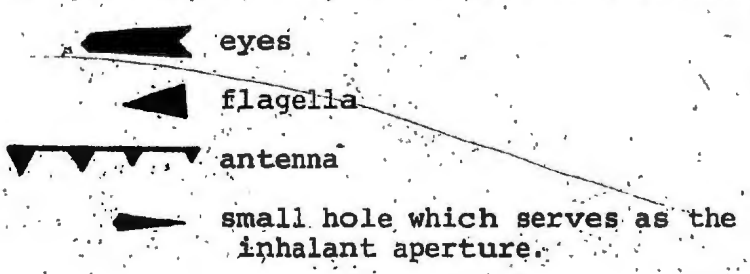
When burrowing the sand shrimp displaces the substrate away by synchronous and powerful beating of all pleopods. The walking legs extend slightly outward and backward and make shuffling movements; usually the first two pairs of the peraeopods are holding the substrate. When a small, long, hollow has been excavated the animal flexes its body 2-3 times, probably forcing water out of the gill chambers and pushing the substrate out and up. With these movements the substrate is pushed around its sides. As a result the body sinks slowly down and obtains a rather horizontal position with the cephalothorax slightly inclined upwards. This action lasts about 10 sec. but the shrimp remains partially uncovered (Plate 10). After this, continuous movements of the antennae begin, with which the shrimp moves the sand and flattens it around and over its back (Plate 11). This action slows down as the shrimp is covered by the substrate. Finally the long antennae come to rest and remain bent backward along the shrimp's body, the whole procedure lasting about 20 sec. The shrimp is now covered with sand; the two small flagella of the first pair of antennae are projecting out of the sand and the eyes also, which are hardly distinguished from the sand grains (Plate 12).

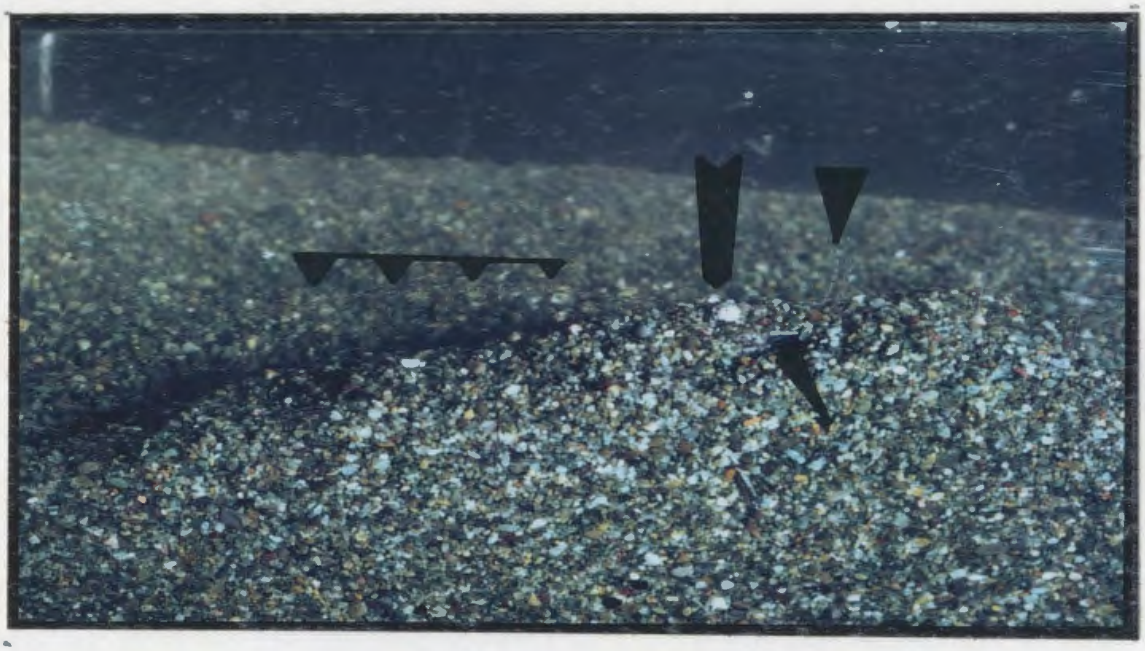
Attempts to put more substrate on the back of the

PLATE 10: The shrimp partially covered in the hollow excavated with the pereiopods.

PLATE 11: The shrimp partially covered with the help of antennae.

PLATE 12: Lateral view of a shrimp almost covered.





animal were not successful. If more substrate is thrown on it, the shrimp rises higher and higher in the substrate so that it is always covered with a very thin layer, not more than a few mm.

It is obvious that the shrimp do not burrow very deep in the substrate, using only a few centimeters from its top. This was also noticed in the field observations.

When the shrimp is burrowed - especially in small particle-sized substrates - the inhalant current is obvious. This was described by Dall (1958) for *Metapenaeus masterit*, Fuss (1964) and Fuss and Ogren (1966) for the pink shrimp *Penaeus duorarum*.

b. Distribution Experiments

Appendix 1 shows the results from the first and second part of this experiment. Results were subjected to a chi-square test of the null hypothesis that the shrimp frequented all sections of the tank randomly, according to the expected Poisson distribution. The possibility that there could be a larger value of chi-square was > 0.05; the hypothesis of random selection was accepted in both parts of the experiment; the animals, under uniform conditions had no preference, and the easier method of releasing the shrimp in the middle of the tank was adopted for the next experiments.

2. Particle-size selection.

Appendices 2, 3 and 4 and Figure 7 give the results of the three replications of substrate particle-

Figure 7

The number of *C. septemspinosa* in the various substrates, summed for the three replications.

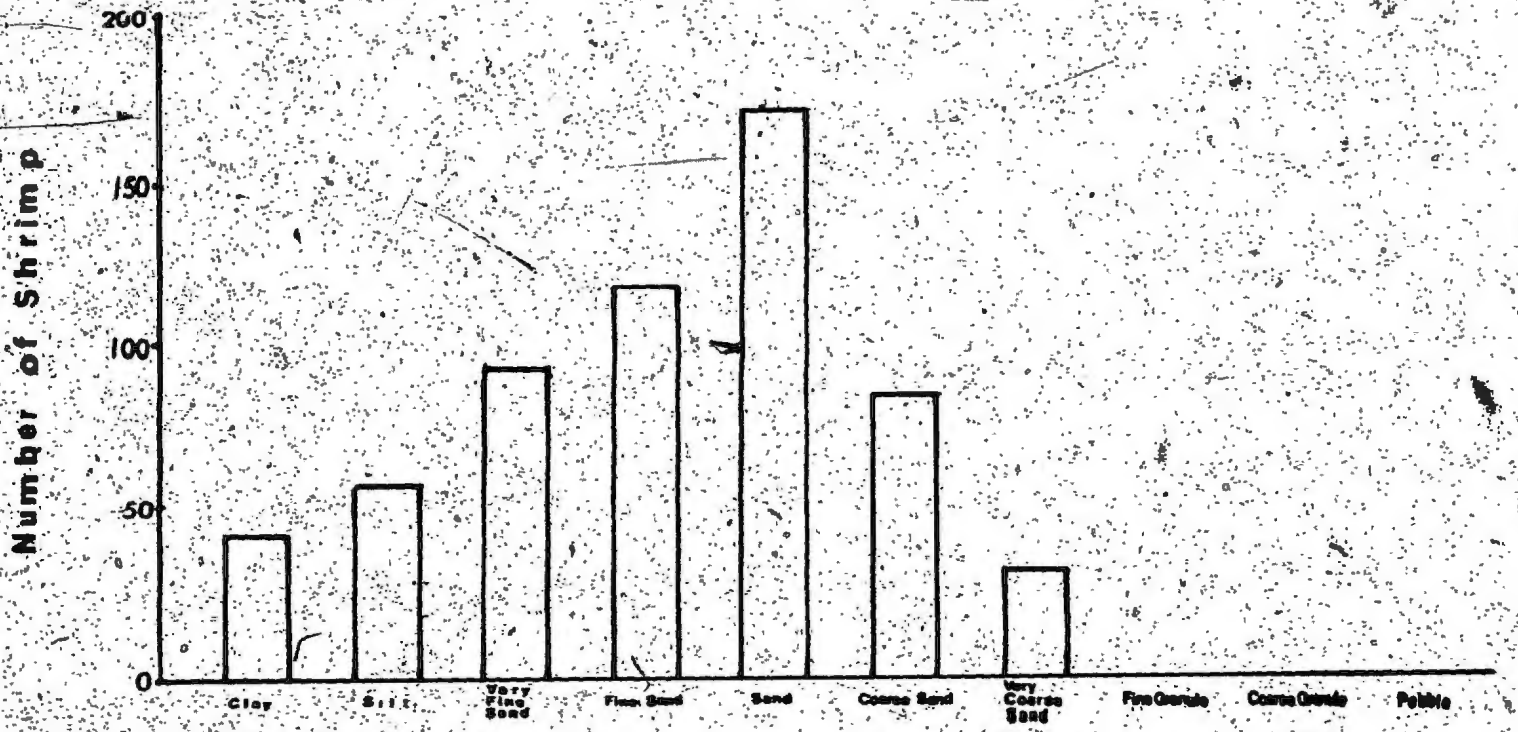
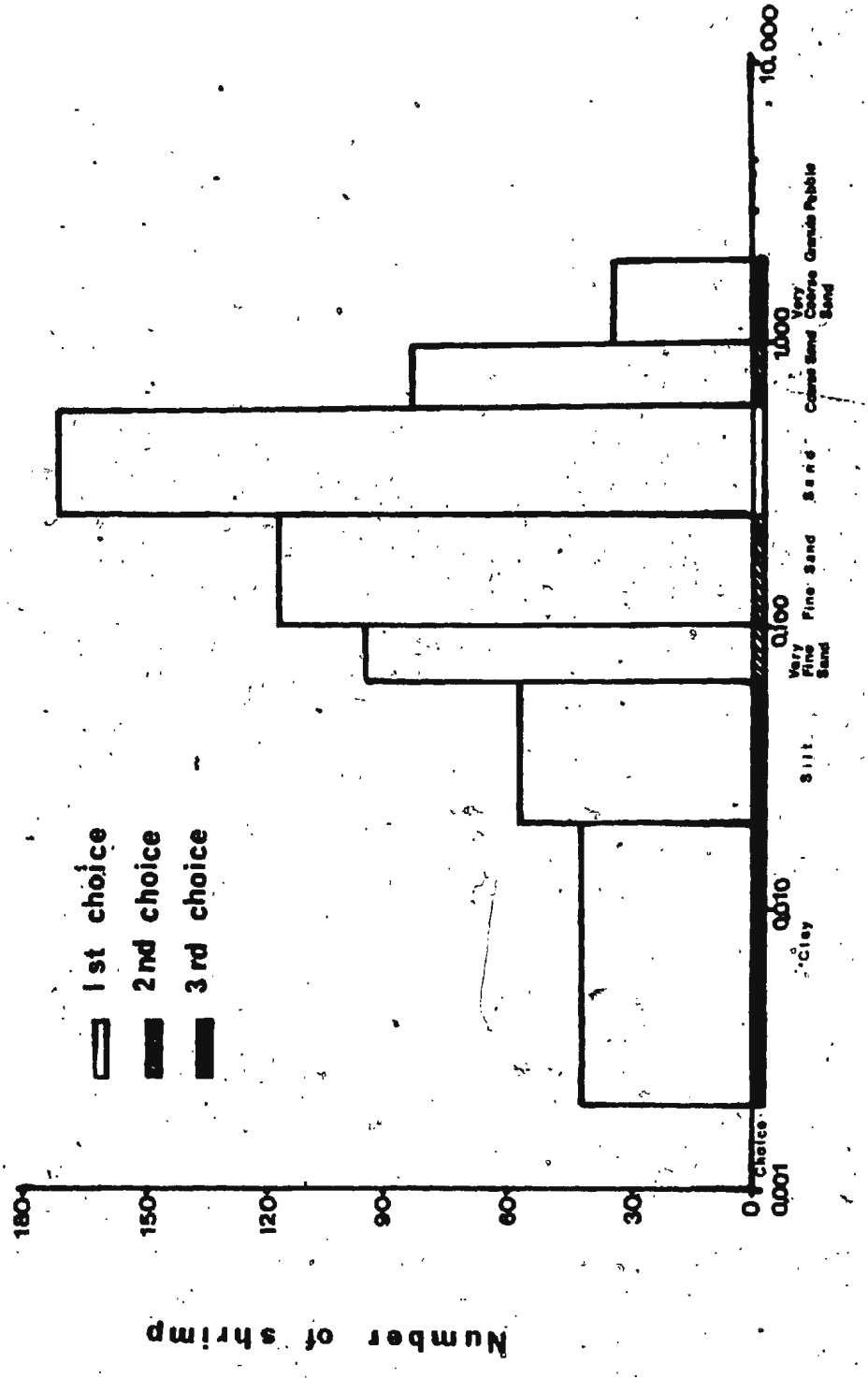

200
150
100
50
0
Number of Shrimp
Clay
Silt
Very Fine Sand
Fine Sand
Sand
Coarse Sand
Very Coarse Sand
Fine Granule
Coarse Granule
Pebble
Substrates

Figure 8

The distribution of *Crangon septemspinosa* in the various substrates, and their degree of choice.


Number of shrimp
180
150
120
90
60
30
0
1st choice
2nd choice
3rd choice
0.001
0.010
0.100
1.000
10.000
Clay
Silt
Very Fine Sand
Fine Sand
Sand
Coarse Sand
Very Coarse Sand
Granule
Pebble
Particle sizes (mm)

size selection experiments.

A chi-square test was applied to test the null hypothesis that the animals selected all of the ten substrate choices in random fashion, according to the expected Poisson frequencies. The probability that there could be a larger value of chi-square was <0.05; the hypothesis of random selection was rejected in the particle-size selection experiment.

The animals selected substrate material from 0.002 to 2.000 mm. Figure 7 shows that more animals preferred sand, followed by fine sand, very fine sand, course sand and finally, silt, clay and very coarse sand. The statistically similar choices are marked on Figure 8 which also shows the distribution of the animals on semi-logarithmic scale. It is clear that the attractiveness of the particle sizes next to the sand is smaller, and choice for particle sizes further on the measuring scale is even more reduced. Selectivity towards bigger particle sizes falls abruptly and no shrimp were found to burrow in substrates bigger than 2 mm. Small particle selectivity decreases smoothly, indicating that the shrimp may burrow in smaller particle-sized substrates.

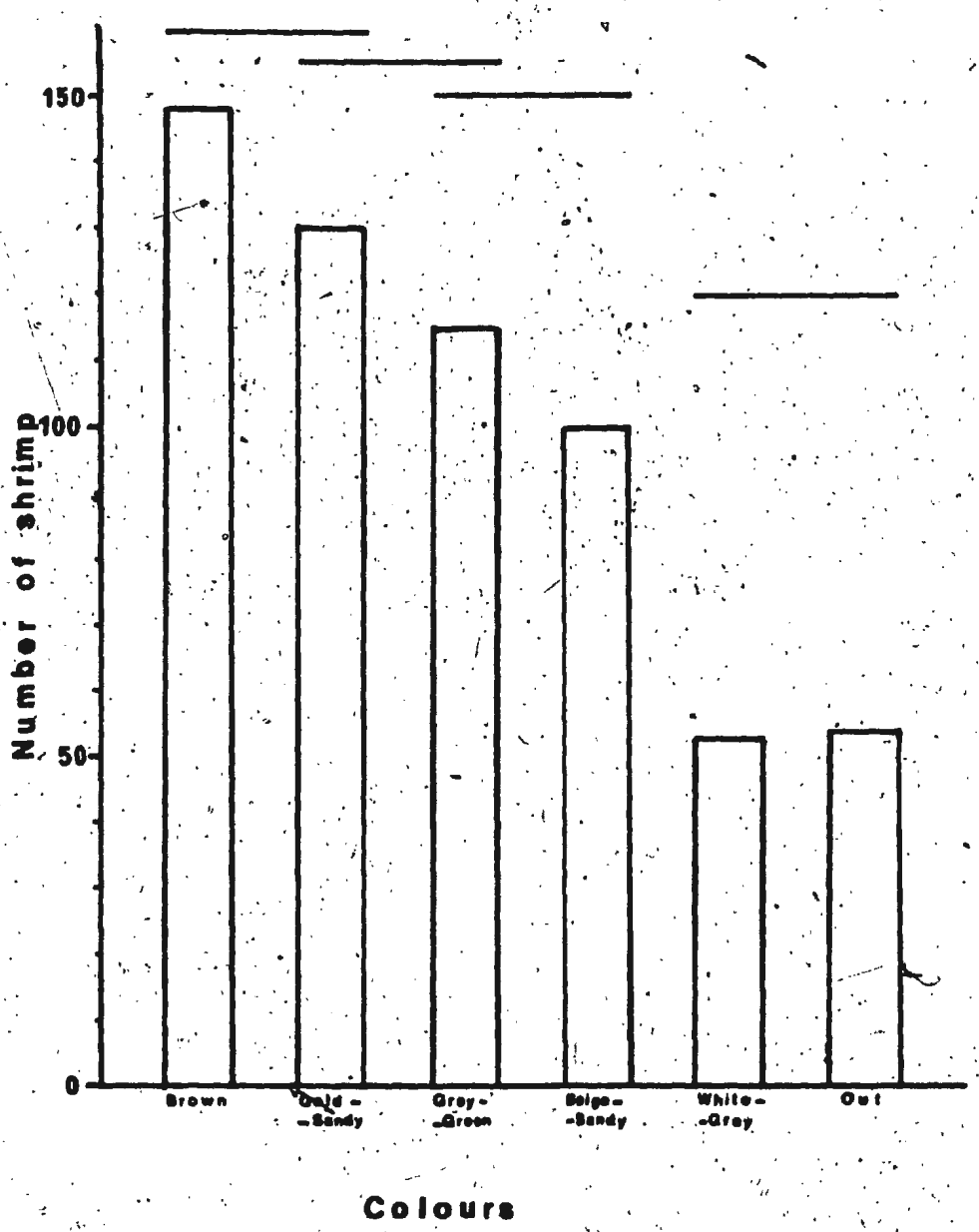
3. Substrate-colour selection.

Appendices 5, 6 and 7 and Figure 9 give the results of 3 replications of substrate-colour selection.

A chi-square test was applied to test the null hypothesis that animals selected all of the five substrate

Figure 9

The number of *C. septemspinosa* in the various substrate colours. Horizontal lines indicate statistically similar choice.


150
100
50
0
Number of shrimp
Brown
Gold - -Sandy
Grey- -Green
Beige- -Sandy
White- -Grey
Out
Colours

choices randomly, according to the expected Poisson frequencies. The probability that there could be a large value of chi-square was 0.05; the hypothesis of random selection was rejected in the colour selection experiment. The shrimp showed preference and they are attracted by the colour of the substrate.

The animals selected the colour brown as their first preference, following by gold-sandy, green-grey, beige-sandy and white-grey. The statistically similar choices are shown with horizontal lines in Figure 9.

In both experiments differences between the replications were observed but, when tested, none of them was statistically significant.

Daily measurements of salinity, conductivity and pH of the running sea water showed little variation in their values.

Trials run in different temperatures showed no differences in the results.

C. Feeding Experiments

Growth was measured as increase in weight, increase in length, moulting frequency and growth rate. Survival of the animals was also determined.

1. Increase in the Weight and the Length

The computed regression equations for the weight and length Hiatt diagrams for each diet are shown in Table 9. The equations for the single diets of the first feeding

TABLE 9

Regression equations for the Weight and the Length in the various diets for both the feeding experiments.

DIETS	WEIGHTS	LENGTH
Squid I	y = 1.7688330 + 1.062268x	y = 1.8681554 + 1.0024554x
Squid II	y = 5.4579788 + 0,97834299x	y = 9.0847207 + 0.82701186x
Mussel I	y = 9.0192796 + 1.0065578x	y = 6.7889822 + 0.90955460x
Mussel II	y = 11.457386 + 0.98310186x	y = 7.0221834 + 0.92144672x
Caplin I	y = 5.4889940 + 0.96920955x	y = 4.7181162 + 0.92213318x
Caplin II	y = 3.5208575 + 0.99614889x	y = 2.3802461 + 0.98727957x
Tetramin	y = 0.9288729 + 1.0383802x	y = 1.5929519 + 0.99042766x
Squid + Mussel	y = 6.2996742 + 1.0361424x	y = 1.9146838 + 1.0263603x
Squid + Caplin	y = 3.8595582 + 0.99931386x	y = 5.7697878 + 0.90241185x
Squid + Tetramin	y = 3.9402988 + 0.99574447x	y = 2.7664438 + 0.9729733x
Mussel + Caplin	y = 6.1533919 + 0.99842508x	y = 5.8217779 + 0.91634354x
Mussel + Tetramin	y = 4.8330386 + 1.0523625x	y = 1.8734801 + 1.0162122x
Caplin + Tetramin	y = 0.92412172 + 1.0311965x	y = 1.0785331 + 1.0016957x
Squid + Mussel + Caplin I	y = 7.4052978 + 1.0193088x	y = 5.5225561 + 0.93578850x
Squid + Mussel + Caplin II	y = 7.5827011 + 0.99580604x	y = 4.7794900 + 0.95823682x
Squid + Mussel + Tetramin	y = 7.6655428 + 1.0073363x	y = 6.5668342 + 0.90573573x
Squid + Caplin + Tetramin	y = 3.3799389 + 1.0034771x	y = 2.3401029 + 0.9818437x
Mussel + Caplin + Tetramin	y = 4.8913255 + 1.0283324x	y = 6.1747904 + 0.90926731x
Squid + Mussel + Caplin + Tetramin	y = 7.5002547 + 0.97817966x	y = 4.9453861 + 0.89077213x
Starved I	y = 1.5319074 + 0.94553920x	y = 4.9453861 + 0.89077213x
Starved II	y = 0.0074149838 + 0.97839328x	y = 3.5168556 + 0.91638451x

experiment are plotted in Figures 10 and 11.

The results from all the comparisons made show that:

i. There is no significant difference between males and females on the same diet in the weight and the length increments.

ii. There are no significant differences in the regression lines of the first and second feeding experiments with the same food, except for the shrimp fed squid. The reason for this difference was not understood.

For comparison purposes, the average pre-moult length and weight of all animals in the first feeding experiment was calculated, being 41.27 mm and 0.59 g respectively. These figures were fitted to the regression equations of Table 9 and the calculated results are shown in Figure 12 for the weight and Figure 13 for the length. It is interesting to notice the similarities of the results in the weight and length, although the measurements of the first are based on a time basis and the second, on the moulting.

Statistical differences between the diets exist. These are shown in Appendix 8 for the weight and Appendix 9 for the length. The pattern of similarities and statistical differences is complex. However, from these results it can be seen that the best increments were given by the diets with mussel and all the combinations of foods with it. In Figures 12 and 13 no diet with mussel

Figure 10

The growth diagrams for the weight - on a 15 day basis for the single diets and the starved.

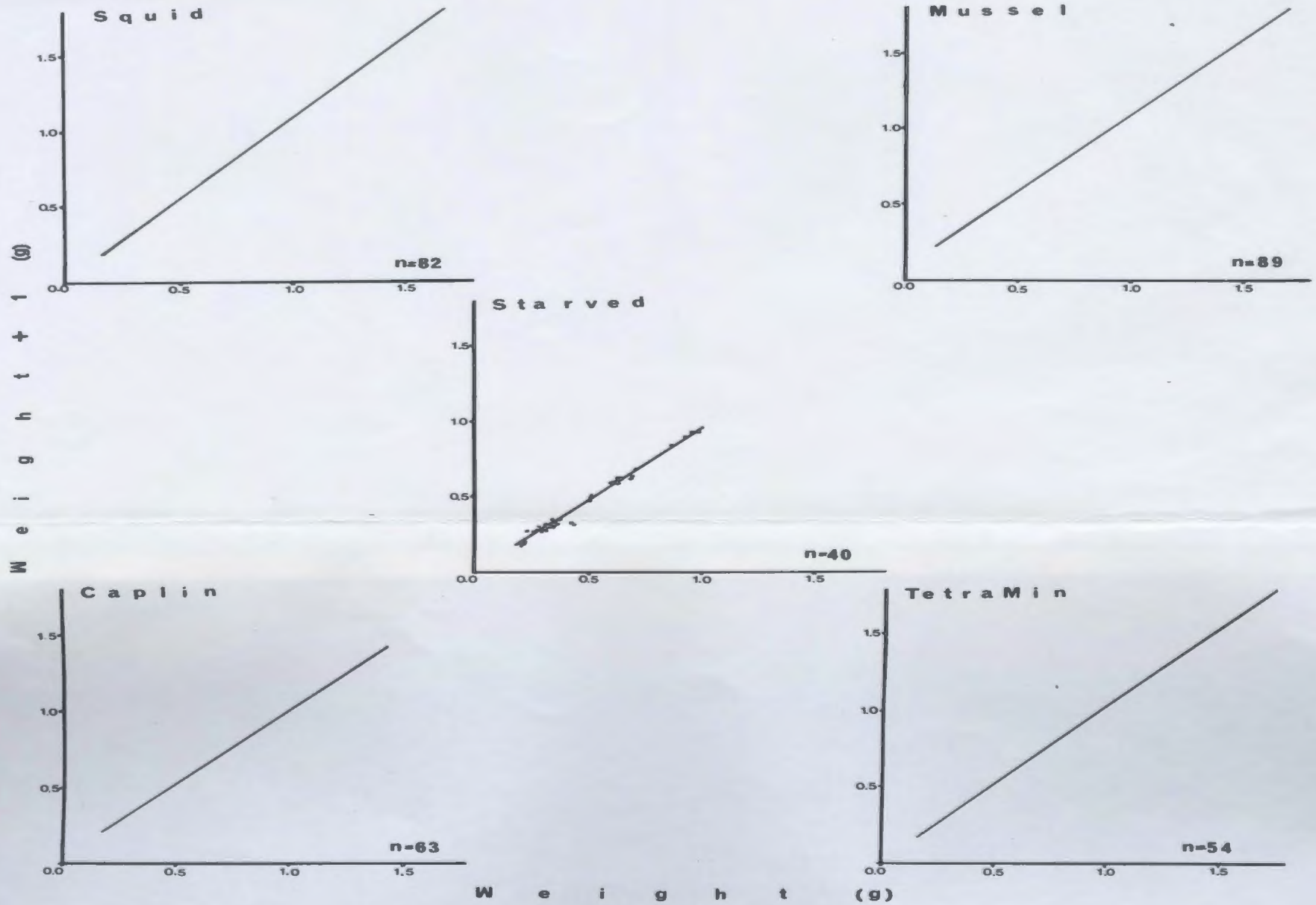

Squid
n=82
Mussel
n=89
Starved
n=40
Caplin
n=63
TetraMin
n=54
0.0
0.5
1.0
1.5
Weight t + 1 (g)
Weight (g)

Figure 11

The Hiatt growth diagrams for the length in the single diets and the starved.

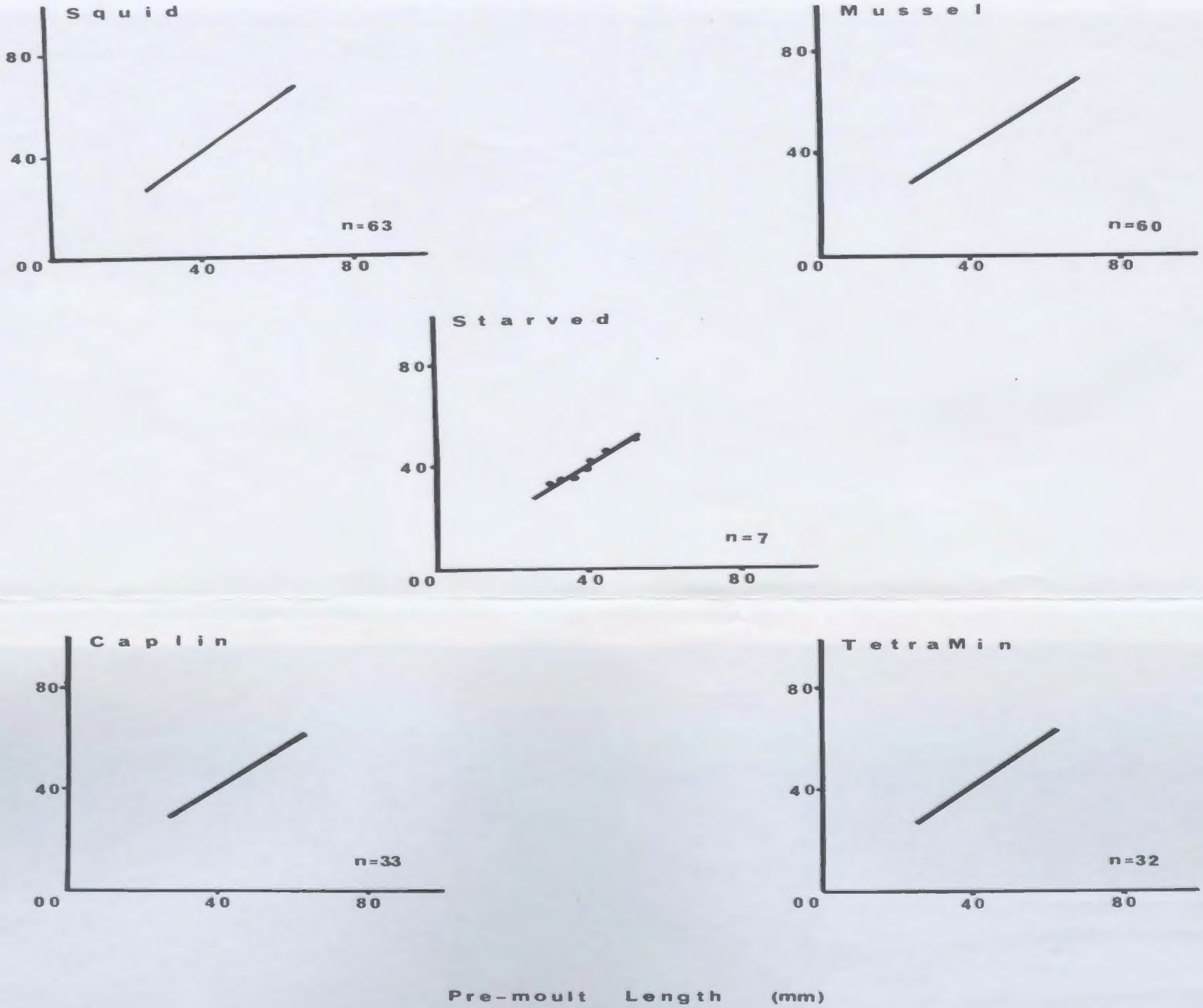

Squid
80
40
00
40
80
n=63
Mussel
80
40
00
40
80
n=60
Starved
80
40
00
40
80
n=7
Caplin
80
40
00
40
80
n=33
TetraMin
80
40
00
40
80
n=32
Post-moult Length (mm)
Pre-moult Length (mm)

Figure 12

Comparative weights in the diets for the average initial weight 0.59 gr.

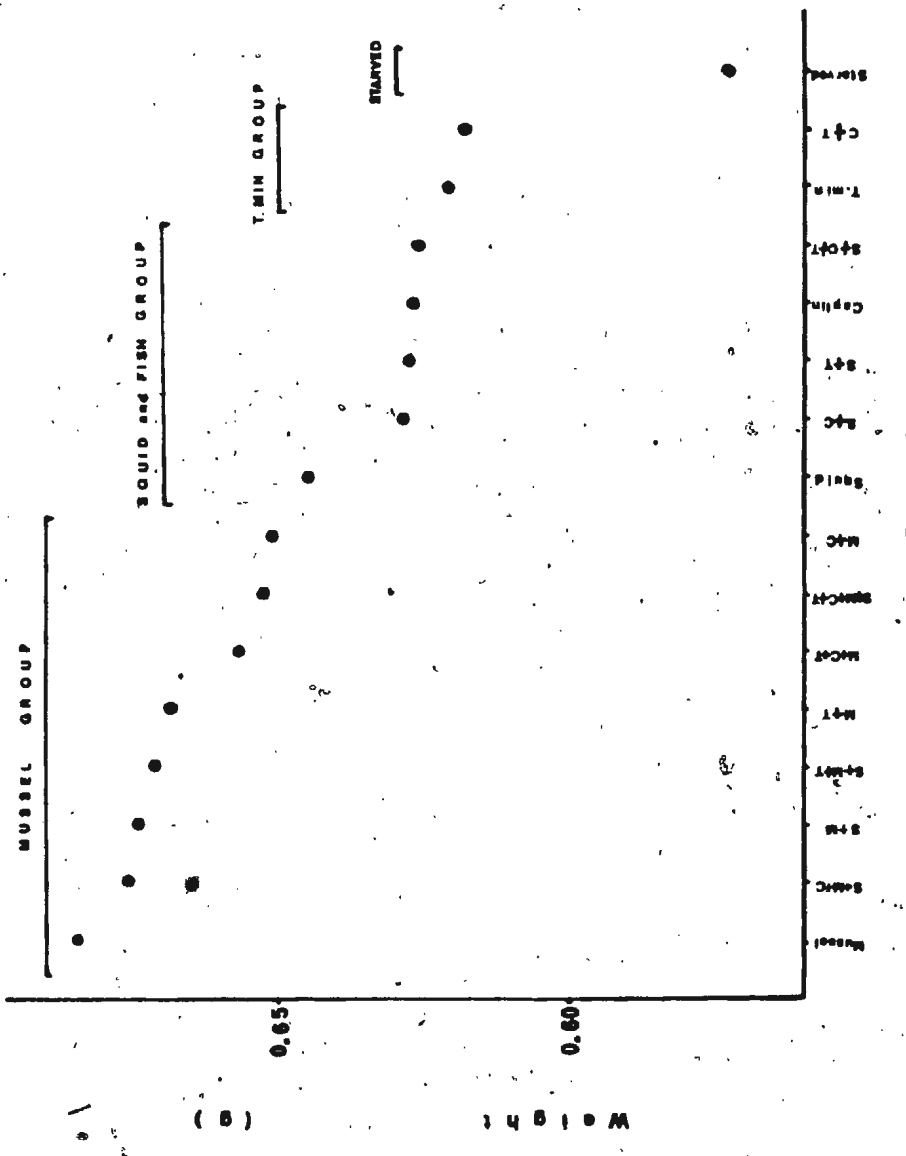
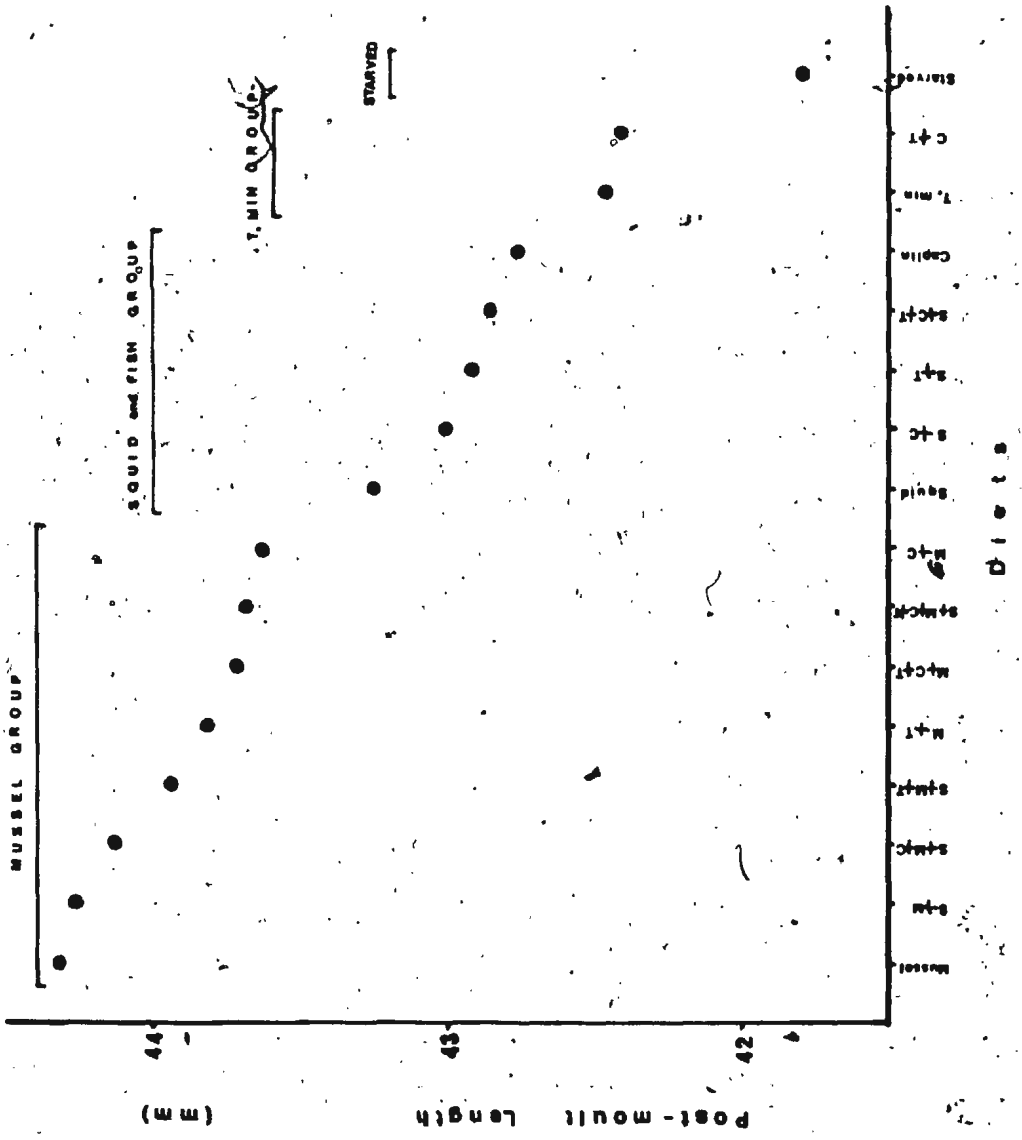

MUSSEL GROUP
SQUID and FISH GROUP
T.MIN GROUP
STARVED
0.65
0.60
Weight
(g)
Days

Figure 13

Comparative post-moult length of the diets for the average pre-moult length 4127 mm.


MUSSEL GROUP
SQUID and FISH GROUP
T. MIN GROUP
STARVED
Post-moult Length
(mm)
Diets
mussel
s+w
s+mc
s+mc?
M+T
Mc+T
s+mc?
M+c
squid
s+c
s+T
sc+T
Capito
T. min
C+T
starved
44
43
42

appears after the diet of squid. Then, all the remaining combinations with squid and caplin appear. TetraMin appears wherever it is combined with squid. These diets gave smaller increments than those including mussel. Smallest increments in the weight and the length were observed in diets of TetraMin and its combination with caplin. Finally, the smallest growth was observed in the starved lot. In the weight there is no diet similar to it; all diets have significant difference with it. For the length, similarities were found in the diets TetraMin and C+T.

From these similarities and the significant differences it is possible to classify the treatments and distinguish four groups.

α'. Mussel group, which includes the diets, Mussel, S+M+C, S+M, S+M+T, M+T, M+C+T, S+M+C+T, M+C.

β'. Squid and Fish group, which includes the diets, Squid, S+C, S+T, Caplin, S+C+T.

γ'. TetraMin group, which includes the diets, TetraMin, C+T and

δ'. Starved group.

The groups are marked on Figures 12 and 13. Although minor differences in the position of each diet within the groups exist, the groups are still separate from each other.

According to Lockwood (1969) and Wilcox and Jeffries (1974, 1976), starvation of *Crangon* spp. can still result in moulting and growth. Hydration levels are also

high in starved shrimp who are not ingesting adequate amounts of food and, presumably, water replaces metabolized tissues. This may be the reason for the small increase of length in the starved group in the experiments, and this may have resulted in the non significant differences with TetraMin and C+T, which appear to be poor diets.

2. Amino acid analyses.

Although the objective of this study was not to deal with food composition, amino acid analyses were made to clarify whether the amino acid composition of the diets could be correlated with growth.

Phillips and Brockway (1956) and Ogino (1963) suggested that the feed having an essential amino acid composition similar to that of the objective animal would be the best. Deshimaru and Shigeno (1972) supported this suggestion and showed a close relation between the distribution of the amino acids, especially the basic ones, of the body of the animal under study; and the feed efficiency of the diet.

The results of the amino acid analyses are shown in Table 10. The compositions were comparable to Deshimaru and Shigeno (1972): glutamic acid predominates and aspartic acid follows. Leucine, lysine and arginive range from ~5-10%, while methionine and histidine range from 2-3%. Their ranges in the table of the Japanese authors are 16-18%, 11-14%, 7-9%, and 1-3% respectively.

The similarity of the amino acid composition

TABLE 10

Amino acid composition of the single diets and the shrimp

	Shrimp		Mussel		Squid		Caplin		Tetramin	
	% (*)	Ratio (**)	%	Ratio	%	Ratio	%	Ratio	%	Ratio
Aspartic acid	6.744	12.967	5.032	11.399	5.440	11.109	6.150	11.606	2.241	8.647
Threonine	2.257	4.340	2.669	6.146	2.312	4.722	2.380	4.492	1.045	4.033
Serine	2.214	4.257	2.258	5.155	2.056	4.199	2.373	4.478	1.232	4.755
Glutamic acid	6.718	12.917	5.813	13.168	8.422	17.198	6.972	13.157	5.385	20.777
Proline	1.930	3.710	2.006	4.544	1.633	3.384	1.923	3.629	2.015	7.746
Glycine	2.479	4.767	1.992	4.513	1.731	3.535	3.073	5.799	1.725	6.666
Alanine	2.764	5.315	2.132	4.830	2.765	5.646	3.678	6.942	1.355	5.228
Half Cysteine	0.406	0.782	0.325	0.736	0.331	0.635	0.372	0.702	0.107	0.415
Valine	3.185	6.124	2.555	5.798	2.408	4.917	2.973	5.610	1.255	4.843
Methionine	1.321	2.540	1.165	2.639	1.376	2.810	1.699	3.206	0.566	2.184
Isoleucine	2.752	5.290	2.217	5.042	2.605	5.320	2.236	4.420	0.949	3.662
Leucine	3.942	7.580	3.237	7.337	4.184	8.544	4.695	8.861	1.899	7.327
Tyrosine	2.312	4.446	1.863	4.220	1.504	3.079	1.693	3.194	0.630	2.430
Phenylalanine	2.962	5.690	2.129	4.833	1.863	3.809	2.965	5.595	0.958	3.696
Lysine	4.077	7.839	3.661	8.294	4.751	9.702	4.827	9.109	1.486	5.734
Histidine	1.635	6.036	1.086	2.470	1.001	2.044	1.313	2.478	0.515	1.987
Arginine	3.059	5.882	2.379	5.399	3.247	6.631	2.917	5.505	1.669	6.439
NH_3	0.831	1.601	0.671	1.623	0.639	1.305	0.530	1.000	0.567	2.198
Cysteic acid	0.047	0.091	0.036	0.082	0.058	0.119	0.035	0.066	0.042	0.163
Taurine	0.105	0.202	0.368	0.834	0.158	0.323	0.063	0.118	0.072	0.278
Hydroxyproline	-	-	-	-	-	-	-	-	0.205	0.792
Citrulline	-	-	0.105	0.238	-	-	-	-	-	-
Cystathionine	0.049	0.094	0.036	0.081	0.018	0.037	0.029	0.055	-	-
Hydroxylysine	0.057	0.110	0.006	0.013	0.041	0.084	0.045	0.084	-	-
γ-Aminobutyric	-	-	-	-	0.006	0.012	-	-	-	-
Ornithine	0.055	0.106	0.164	0.372	0.100	0.204	0.011	0.021	-	-
Ethanolamine	0.077	0.148	0.084	0.191	0.266	0.543	0.039	0.073	-	-
3-Methylhistidine	0.028	0.054	0.019	0.043	0.034	0.069	-	-	-	-
TOTAL	52.006	100	44.143	100	48.969	100	52.986	100	25.918	100

(*) Amount of amino acids in dry weight of crude protein residue
(**) Composition rate of each amino acid to total amount of amino acids in the residue part

TABLE 11

Similarity of the amino acid composition pattern of the single diets to that of shrimp

Amino acid	Mussel	Squid	Caplin	TetraMin
Aspartic acid	-	-	-	-
Threonine	+	*	*	*
Serine	+	*	*	*
Glutamic acid	*	+	*	+
Proline	+	*	*	+
Glycine	*	-	+	+
Alanine	*	*	+	*
Half Cysteine	*	*	*	*
Valine	*	-	-	-
Methionine	*	*	+	*
Isoleucine	*	*	-	-
Leucine	*	+	+	*
Tyrosine	*	-	-	-
Phenylalanine	-	-	*	-
Lysine	*	+	+	-
Histidine	-	-	-	-
Arginine	*	+	*	+
Cysteic acid	*	*	*	*
Taurine	+	*	*	*
Cystathionine	*	*	*	0
Hydroxylysine	*	*	*	0
Ornithine	*	*	*	0
Ethanolamine	*	*	*	0
3-Methylhistidine	*	*	0	0
Similar amino acids	17	14	13	8

* Similar amino acid composition-rate within the range of ± 0.5% from that of the shrimp

\+ Over the range

\- Below the range

0 No amino acid

pattern of the diets to that of the sand shrimp is presented in a simplified way in Table 11.
The amino acid composition in the mussel is closest to that of the shrimp. TetraMin has a composition far different from that of the shrimp, being short in indispensable amino acids such as isoleucine, phenylalanine, lysine and histidine. Squid and caplin are intermediate.

3. Moulting and Moulting frequency

The moulting frequency at the water temperature of 13°C was estimated from the records of the animals and it is given in Table 12 for the four groups. For this purpose the animals were classified in size classes according to their length. Animals of 30-39 mm in total length were put in the III size class and animals of 40-49 mm, in the IV size class.

TABLE 12

Moulting frequency ± confidence limits of *Crangon septemspinosa* at 13°C in days

Diet groups	III Size Class (30-39 mm)	IV Size Class (40-49 mm)
Mussel group	17 ± 1	20 ± 1
Squid and Fish group	20 ± 2	24 ± 2
TetraMin group	21 ± 2	25 ± 3
Starved group	minim. 42 ± 7	minim. 47 ± 11

The intermoult period of the starved group is hypothetical, given only for comparison purposes. It was estimated on the basis of survival from the day of the observed moulting - if any - up to the death of the shrimp.

The Mussel group has the shortest intermoult period; the same periods for the two remaining groups are intermediate and greatly overlap, probably because there is not much difference in their nutritive value.

The moulting frequency was estimated separately for the males and females in the two size classes for the diets of the long-term experiment and the common diets of the two feeding experiments. This is given in Table 13 and Figures 14 and 15. These figures show that the intermoult period at the same temperature (i) increases with the increasing size, i.e. bigger shrimp would moult less frequently than the smaller ones; (ii) increases towards less effective diets, and (iii) there is an indication that female shrimp would moult more often than the males in diets with high nutritional value and less frequently in diets with lesser nutritional value.

Mortalities occurred during moulting; the moult failures observed in the tanks were classified in three categories:-

i. Direct-fatal moult failure: The shrimp were found dead in the tanks in the morning. In all the cases the carapace part of the old exoskeleton was found incompletely detached and covering the head of the shrimp. No matter if

TABLE 13

Molting frequency

Mean day ± Confidence limits/sex/size class

DIETS	SEX	III size class + Confidence Limits	IV size class + Confidnece Limits
Mussel	♂	15.81 ± 1.32	21.03 ± 1.01
	♀	16.08 ± 1.52	18.15 ± 0.96
S+M+C	♂	17.50 ± 1.38	21.08 ± 0.88
	♀	17.31 ± 2.59	20.00 ± 2.10
Squid	♂	18.21 ± 1.58	21.53 ± 1.20
	♀	17.69 ± 1.90	22.60 ± 2.92
Caplin	♂	20.22 ± 2.30	23.95 ± 1.62
	♀	21.50 ± 5.00	28.00 ± 3.58
Starved	♂	36.00 ± 7.89	37.50 ± 14.84
	♀	47.70 ± 12.64	50.29 ± 18.74

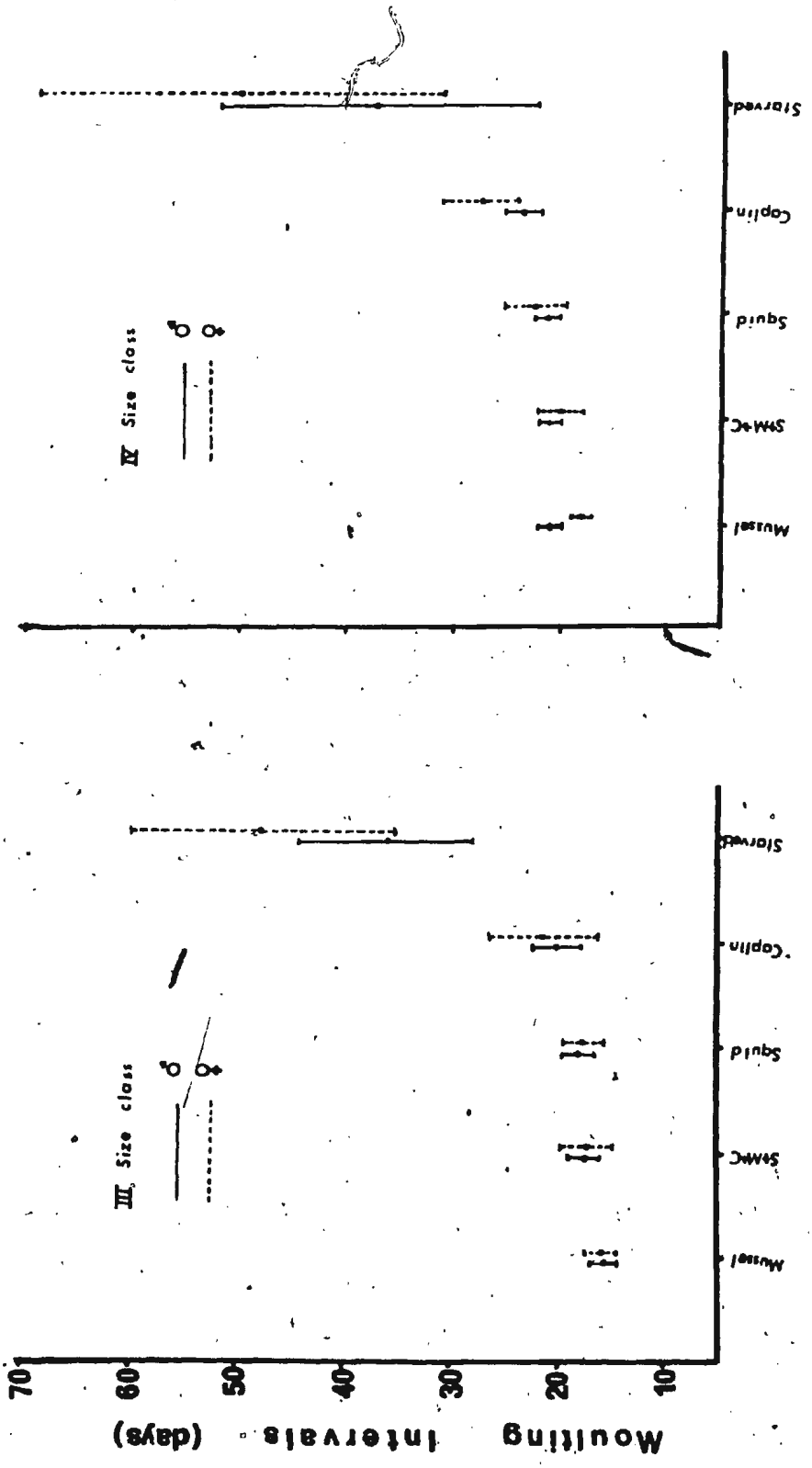
Figure 14

Moulting intervals for the common diets of the feeding experiment. Days ± Confidence limits per sex and per size class.

DIETS
Mussel
Shrimp
Squid
Caplin
Sloread
MALES
Size class III
Size class IV
FEMALES
Size class III
Size class IV
Moulting Intervals (days)
10
20
30
40
50
60
70

Figure 15

Moulting intervals for the common diets of the feeding experiments: Days ± Confidence limits per sex in the III and IV size classes.


Molting intervals (days)
10
20
30
40
50
60
70
Mussel
Shrimp
Squid
Copiin
Starved
III Size class
♂
♀
IV Size class
♂
♀
DIETS

the shrimp was able to free itself from the abdomimal part of the cuticle, death occurred invariably within a few hours.

ii. Indirect-fatal moult failure: In this case the shrimp were able to free themselves from all the other parts of the old exoskeleton, except the lower front one. They were not able to withdraw their 2nd and 3rd maxillipeds and pereiopods from the old cuticle which remained there, keeping all these parts tied together. The shrimp were not able to burrow and usually remained above the substrate; they were lying on their side, making occasional spasmodic movements trying to free themselves from the exoskeleton. After 2 to 4 days, the shrimp died, probably because of breathing difficulties.

iii. Partial-moult failure: The moulting in this case was almost regular. The shrimp were able to free themselves from the front part of the exoskeleton but not from the abdominal part. The behaviour of these animals was normal during eating and burrowing. They were active and seemed healthy. However, the remaining part of the old cuticle was absorbing water and day by day it was turning to opaque. From the records kept it was noticed that all these shimp invariably died after they passed the day of their expected moult. None of them survived to moult again. The cause of these deaths was not understood. The exact physiological mechanism of hydration is unknown, but perhaps it involves the hormones of the moult cycle (Passano, 1960, from Wilcox, 1972).

4. Growth rate

As an overall check of the results of the weight, length, and moutling frequency, the growth rates per week for the animals in the various diets was determined. This was calculated from the moulting frequency and the increments of length between moults, in relation with the number of observations in each diet or group. These growth rates for each diet and group are shown in Table 14. Size classes and sexes are separated in the table, and the numbers of observations are marked. For more detailed data, Appendix 10, separates the first from the second feeding experiment. As can easily be seen from the growth rates the classification of the diets in the order and the groups stated is justified.

Table 15 gives comparisons of the sexes and the groups. It is shown in the table that the growth rate of the smaller animals (III size class) is higher than the bigger animals (IV size class). As a general rule, the growth rate is smaller in less effective diets and the males have smaller growth rate than the females. The latter happens with the exception of low efficient diets, ie. TetraMin group and Starved group.

TABLE 14

Growth rate per week in mm for the diets and the groups.

	DIETS	III size class			IV size class			III and IV size class
		MALE N	FEMALE N	♂+♀ of the class (*) N	MALE N	FEMALE N	♂+♀ of the class (*) N	Average of classes (**) N
Mussel Group	Mussel	2.3527002 17	1.5546931 19	1.9315297 36	0.8683518 38	1.3798944 27	1.0808387 65	1.3840552 101
	S+M+T	1.5489361 14	1.666666 3	1.5697119 17	0.9079497 13	0.9444443 7	0.9207228 20	1.2189069 37
	S+M	1.0547945 12	1.8958333 3	1.2230022 15	0.9514563 11	1.050000 2	0.9666168 13	1.1039661 28
	S+M+C	1.1094791 17	1.6991963 14	1.3758029 31	0.7149341 33	1.0816803 15	0.8295422 48	1.0438976 79
	S+M+C+T	1.1838235 16	0.9390243 5	1.1255379 21	0.7074468 10	0.995098 9	0.8437026 19	0.9916661 40
	M+C+T	1.0652173 8	0.777777 5	0.9546635 13	1.0689655 11	0.5505617 4	0.9307244 15	0.9418389 28
	M+C	0.7894736 13	1.6030534 8	1.0994087 21	0.7368421 9	0.6470588 5	0.7047766 14	0.9415557 35
	M+T	0.723333 16	2.1724137 2	0.8843421 18	0.7692307 14	1.166666 11	0.9441022 25	0.9190863 43
	Average for the Mussel Group	1.2610555 113	1.5215023 59	1.3504062 172	0.8280104 139	1.1177527 80	0.9338522 219	1.1170933 391
Squid and Fish Group	Squid	1.0615383 26	0.8428323 15	0.9815238 41	0.4406998 31	0.8358134 15	0.5695411 47	0.7636939 87
	S+C	0.7179487 6	1.1226415 6	0.920295 12	0.3987341 7	0.7403846 5	0.5329706 11	0.7302702 23
	S+C+T	0.5875918 14	1.00000 2	0.6391428 16	0.2692307 1	1.0208333 2	0.7702991 3	0.6598516 19
	S+T	0.715555 12	0.4117647 3	0.6547973 15	0.4516129 12	0.7403846 5	0.5365457 17	0.5919761 32
	Caplin	0.6303523 13	0.5189586 3	0.6045108 14	0.3256308 16	0.3535305 9	0.3356746 25	0.4321798 39
	Average for the Squid+Fish group	0.8066703 69	0.8334656 29	0.8142593 98	0.4082315 67	0.6978314 35	0.5075738 102	0.6578496 200
Tetramin Group	Tetramin	0.5051546 9	0.53030303 6	0.5152139 15	0.424242 3	0.2658227 3	0.3450325 6	0.4665906 21
	C+T	0.4958333 12	0.4827586 3	0.4932183 15	0.2413793 4	0.3043478 1	0.253973 5	0.4334069 20
	Average for the Tetramin Group	0.4998281 21	0.5144548 9	0.5042161 30	0.3197492 7	0.2754539 4	0.3036418 11	0.4504034 41
Starved	Starved	0.2665231 4		0.2665231 4		0.122807 4	0.122807 4	0.194665 8
	Average for the Starved	0.2665231 4		0.2665231 4		0.122807 4	0.122807 4	0.194665 8

(*) $\frac{\text{(Growth rate of ♂ x ♯ of ♂) + (Growth rate of ♀ x ♯ of ♀)}}{\text{(Total ♯ of ♂ and ♀ in the class)}}$ N = number of observations.

(**) $\frac{\text{[Growth rate of III size class x ♯ of (♂+♀)] + [Growth rate of IV size class x ♯ of (♂+♀) of the class]}}{\text{Total ♯ of (♂+♀) in both size classes.}}$

TABLE 15

Growth rate per week in mm per sex and per group.

Size Class	Sex	Mussel group	N	Squid & Fish group	N	Teteramin group	N	Starved	N
III	♂	1.2610555	113	0.8066703	69	0.4998281	21	0.2665231	4
	♀	1.5215023	59	0.8334656	29	0.5244548	9	———	
	♂ & ♀	1.3504062	172	0.8142593	98	0.5042161	30	0.2665231	4
IV	♂	0.8280104	139	0.4082315	67	0.3197492	7	———	
	♀	1.1177527	80	0.6978314	35	0.2754539	4	0.122807	4
	♂ & ♀	0.9338522	219	0.5075738	102	0.3036418	11	0.122807	4
III & IV	♂	1.0221933	252	0.6101354	136	0.4548083	28	0.265231	4
	♀	1.2891284	139	0.7592425	64	0.440916	13	0.122807	4
	♂ & ♀	1.1170933	391	0.6578496	200	0.4504034	41	0.194665	8

N = number of observations. Calculations as in Table 14.

5. Survival

Daily observations disclosed the survival within all the diets. Appendix 11 gives the days of survival for the diets in the first and long-term feeding experiments and Appendix 12, for the second feeding experiment. The per cent survival in the common diets of the two feeding experiments was combined with the survival in the long-term experiment and is shown in Figure 16. In this figure it is shown that mussel, as a diet, had higher survival than all the diets, including the diets in its group; S+M+C has lower survival than mussel. The survival of caplin is lower than that of squid, and the survival of the starved animals is the lowest.

The Mann-Whitney U-test was applied for the common diets of the first and second feeding experiment to test the survival of males and females in each diet. There was no significant difference at $P = 0.05$ in the diets. Only the starved females showed significantly higher survival than the males.

As regards to the survival on diet groups, because no shrimp of the dietary groups γ' and δ' survived for 16 weeks, mortalities are also given for a period of 12 weeks for comparison purposes in Table 16:-

Figure 16

Percent survival in the common diets of the two feeding experiments combined with the survival in the long-term experiment. Line (A) indicates the duration of the 1st and 2nd feeding experiment.

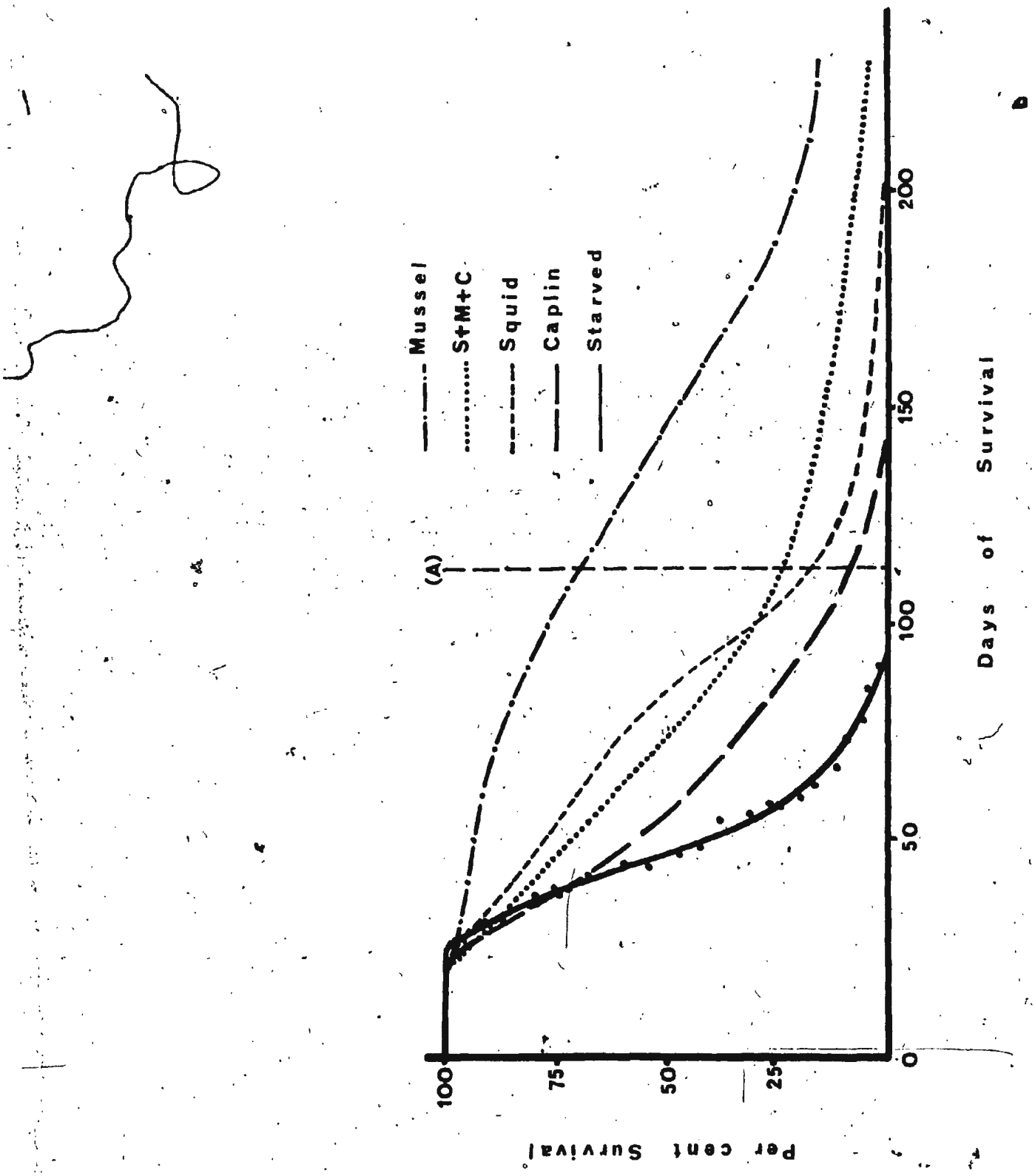

Mussel
St+M+C
Squid
Caplin
Starved
(A)
Per cent Survival
100
75
50
25
0
50
100
150
200
Days of Survival

TABLE 16

Approximate per cent mortalities of *Crangon septemspinosa* in the diet groups.

Diet Groups	MORTALITIES	
	12 weeks	16 weeks
α' Mussel group	35%	55%
β' Squid and Fish group	60%	86%
γ' Tetramin group	70%	100%
δ' Starved group	95%	100%

In all the diets the shrimp appeared healthy and active. Usually they were buried in the sandy substrate of their cages and they emerged as the food was being placed in them. The most active shrimp were the ones fed with mussel and considerable attention was needed to prevent them from jumping out of their cages into the channel. The survival in this group indicate that, although it is considered as the group with the best diets, deaths would be expected even in these-almost optimum conditions.

Survival was the lowest in the Starved group, which showed progressive nutritionally stressed symptoms. In the first week the starved animals were burrowed in the substrate as the others did, but day by day more and more shrimp were found lying quiescent above the substrate. At about 4 weeks no starved shrimp were burrowed in the substrate. Some shrimp were able to moult in this period;

their exoskeletons were extremely thin and transparent; no shrimp moulted for a second time. At about 5 weeks all of them were hanging on the sides of their cages and, when disturbed, they showed an unusual behaviour by swimming upside-down on the surface of the water. Wilcox (1972) also observed the same behaviour in his food preference studies and described it as an extreme and zealous search for food. At about a week later, all the remaining sand shrimp were resting on the surface of their cages. As it was mentioned, according to Lockwood (1967) and Wilcox and Jeffries (1974,1976) hydration was very high; their exoskeletons were almost opaque. When removed and placed on their backs, only small, weak movements of the pleopods showed that they were alive. They were moribund.

Groups β' and γ' were intermediate. There was a small differences between the two, indicating small differences of the nutritional value of their food.

Moult failure was a reason for a number of deaths in both experiments. The deaths due to moult failure were about 13% of all the dealths in each feeding experiment. When tested, it was found that deaths due to moult failure are a fair fit to Poisson, less than 0.05, so they are a random and independent factor probably, and not diet related.

There was also a significant proportion of mortalities among the shimp, the cause of which could not

be identified. The shrimp were found dead without any indication of moult failure and their body was opalescent, probably due to formation of the new integument beneath the old one. From the records of the shrimp it was easily noticed that these animals died just prior the expected time of moulting. In the second feeding experiment these deaths appeared in the lots fed S+M+C, squid, and caplin. In the S+M+C lot these deaths were 13% of all the deaths in it, in the squid, about 23% and in the caplin, around 39%.

V. DISCUSSION.

A. Field Studies

1. Length-frequency distribution and Population structure.

Egg-carrying female *Crangon septemspinosa* appear in Long Pond from April to August with their main peak in July. The juveniles were always present in the population and were most abundant in August; they increased in size to November and show little further increase until May. After May they appear in the population as mature animals.

According to Squires (1965) and Haefner (1972) the juveniles which appear in August probably were produced in early spring, and the first postlarvae produced in the summer would attain the size of 20 mm in late fall, and 40 mm the following year, after 7-10 months. The number of juveniles collected was small in November and does not indicate a second brood as suggested by Squires and Haefner. High predation and extensive mortality may have been the reasons for the small numbers of juveniles by November. The 40-42 mm animals, found in early spring, were obviously shrimp of the August peak. The appearance of juveniles in April certainly must have resulted from recruitment of late broods produced in fall or early winter.

The fact that juveniles were collected in almost all the collections suggest that they exist during 11-12 months and that their appearance is due to recruitment from an extensive breeding period. It is therefore suggested that egg-carrying females occur for about the same duration.

These animals were collected over a period of five months. However, they suddenly disappeared from the population in September, although they were still carrying eggs in the middle stages of the development in August. This suggests that egg carrying females may exist for a longer period among the segments of the population, but they probably leave the inshore waters in September.

To investigate the complete breeding cycle of *C. septemspinosa* Price (1962) and Haefner (1972) suggested simultaneous shore-zone and deep-water surveys to be conducted, assuming migration of the egg-carrying females.

The observations on the spawning periods for *C. septemspinosa* vary. On Georges Bank in the Gulf of Maine, Whiteley (1948) indicated an annual brood, based on collections of ovigerous females in April, May and June. In the channel of Chesapeak Bay, Cowles (1930) reported ovigerous females during all seasons. In the shore zone of Delaware Bay, Price (1962) suggested March through October as the breeding season. In Port au Port Bay, Squires' (1965) observations indicated at least two broods from May to September. At Lamoine, Maine, Haefner (1972) collected egg-carrying females from May through September; he suggested two broods of shrimp per year and put forward for consideration as a possibility that the individual sand shrimp carry eggs throughout most of the year. The same author, in 1976, concluded that *C. septemspinosa*

exhibits a single but extended breeding season in the southern Chesapeake Bay area.

Female shrimp slightly outnumber the males. Similar observations were also made by Price (1962). However, the phenomenon of the females outnumbering the males may only be accidental and may have nothing to do with the spawning as he suggests. Congregation of sexes and certain size groups, as Meredith (1952) believes for *C. vulgaris*, is a hypothesis which may only be proved by extensive observations or by experimentation.

An overlap was noted from 24 to 27 mm in mature animals and animals with nondifferentiated endopodites. Similar overlap was noted by Price from 22 to 30 mm, who presumed therefore, that the appearance of the differentiated endopodite procedes slightly or coincides with the advent of maturity; he supported Whileley's (1948) presumption that the sand shrimp reaches maturity within one year. The difference in the range of the two studies agree with Meredith (1952) who pointed out that female *C. vulgaris* mature at shorted lengths at lower temperatures and proposed that "... size at maturity is possible related to temperature, not age." Regnault (1970) proposed that, among other factors, the development of the external sexual characteristics and sexual maturity are determined more by size than the age of the shrimp. This permits the conclusion that the development of sexual characteristics is

related to the temperature not age, i.e. the shrimp in Northern latitudes develop their sexual characteristics at shorter lengths then their southern counterparts. The reason for the smaller size at development in Northern latitudes is the slower growth due to cooler temperatures.

The equations relating size, temperature and month, suggest a possible hypothesis for offshore migration during the cooling of the water and inshore migration when the temperature increases. The decrease in the mean length of the population suggests that the bigger shrimp move offshore when the temperature falls, while the juveniles - the length of which does not depend on the temperature according to the equation - remain inshore. Later, when the temperature increases, the larger animals probably move inshore.

Haefner (1976) also hypothesized that when the water temperature decreases in the fall, *Crangon septemspinosa* is stimulated to move from shallow regions to deeper waters. The same author (1972) reports that larger adults disappear from the beaches at the beginning of the winter and most of them are gone by the middle of the season. When the temperature falls only "stragglers" are found inshore. Squires (1965) reports onshore-offshore migration in the Gulf of St. Lawrence. Embich (1973) also reports probable migration when water temperatures reach 5-6^{o}C. In these studies reappearance in the shore zone in the spring was correlated with an increase in temperature above 5^{o}C.

Price (1962) noted an increased mortality rate after the lengths of 52 mm in female and 42 mm in male had been reached, but it was not certain whether disappearance of large shrimp was due to mortality or migration to deeper waters, because his collections were made in water 1.5 m deep or less. Haefner (1976) supports that this was a result of the migration.

The hypothesis of Price (1962) that bigger shrimp die during the cold months may explain the decrease in the length of the population but can not give a complete explanation of the appearance of large egg-carrying shrimp in April. He also reported that the first egg carriers were large females. These are probably shrimp which migrate towards the shore with the increase of the temperature. Further, the absence of females carrying eggs in the last stages of development indicates few hatch in the area sampled. This observation can be possibly explained with the migration of these animals from the coast to deeper, more saline waters, with the progress of egg development. The disappearance of egg-carrying shrimp from the population in September, probably supports the hypothesis for migration of the sand shrimp. An extensive mortality of these animals in September would result in a reduction of the Long Pond population and this does not seem to be true.

The length-frequency distributions and categories of the sand shrimp population throughout the year show that the largest shrimp are females; this happens due to a

a different growth rate of males and females after maturity. The possible maximum age can be estimated as more than two years for males and approximately three years for females. This estimation is in agreement with other information for *C. septemspinosa* (Price, 1962; Embich, 1973). The greatest mortalities probably happen either with the cooling of the waters or after spawning.

B. SUBSTRATE-SELECTION EXPERIMENTS.

1. Preliminary Observations.

a. Burrowing Behaviour.

Fuss (1964), studying the burrowing behaviour of the pink shrimp *Penaeus duorarum*, observed two burrowing methods. The first method has a scouring phase, with which the animal sets up a water current with the pleopods which scours an initial furrow into which the animal settles; then a plowing phase follows with which the shrimp plows ahead into the anterior end of the depression, using the walking legs to force itself into the sediment. The second method of burrowing differs from the first by the elimination of the scouring phase; with the second method the animal plows immediately into the bottom and then settles. Fuss also reports that Egusa and Yamamoto in 1960 mentioned that *Penaeus japonicus* when burrowing use the second method observed. Dall (1958) gave description of the burrowing methods for *Metapenaeus mastersii*, which generally agree with the first method described in Fuss' paper.

Although Dall does not describe the substrate where *M. mastersii* burrow and Fuss (1964) says that the observations for the pink shrimp were obtained on sand-silt-clay bottom, in another paper by Fuss and Ogren (1966) it is confirmed that the pink shrimp have the ability to enter extremely coarse substrates. It is, therefore, noteworthy to indicate that these observations show that these species which are able to burrow in hard substrates use both methods described by Fuss, while species specialized in soft substrates use only the second method.

The first burrowing method of Fuss was not observed in the sand shrimp. *Crangon septemspinosa* digs in the substrate with the pleopods and when it excavates a hole it settles in it and shovels sand with the antennae to cover its back.

Previous observations of burrowing methods of the genus *Crangon* were given by Lloyd and Yonge (1947) for the European species *Crangon vulgaris*. The observations of Lloyd and Yonge fully agree in most details with the observations for *Crangon septemspinosa*. The use of antennae were observed in at least these two Crangonidae, which use only the second burrowing method. It is interesting to notice that both, Fuss and Dall, do not mention the use of antennae in the burrowing methods of the shrimp studied by them. Further, *C. vulgaris* is a species specialized for life on a soft substratum of sand and mud according to Lloyd and Yonge and Meredith (1952). These adaptations were also noted in *C. septemspinosa*.

Observations describing the position of the shrimp in the substrate are scarce. The observations for *C. septemspinosa* show that the shrimp rest in the substrate in a rather horizontal position with an imperceptible degree of inclination of the cephalothorax. This position was described by Dall (1958). According to him the cephalothorax was inclined upwards with only the tips of the antenules and sometimes the tip of the rostrum protruding. However, the degree of inclination of the sand shrimp's cephalothorax is very much smaller than what Dall describes.

The sand shrimp do not burrow deep in the substrate, but only a few millimeters below the surface. All Fuss' measurements show that the pink shrimp penetrate the bottom so that their dorsal surfaces are just below the surface. Williams (1958) suggested that bottom type may influence the depth of burrowing. He found that *Penaeus duorarum* tend to burrow deepest in sand-shell type bottoms, reporting that some animals were often buried as deep as about 5 cm. This is also true for *P. atzecus*, but *P. setiferus* presents a different burrowing aspect than the latter two, for it does not burrow so deep and prefers mudier substrates. *C. septemspinosa* shows similar behaviour and similar preferences with *P. setiferus* and this supports Williams suggestion. Probably shrimp specializing in soft substrate do not burrow very deep.

2. Particle size and colour selection.

The results for the substrate selection experiments indicate that *Crangon septemspinosa* selects sand as their first choice, very fine sand, fine sand and coarse sand as their second choice, and clay, silt and very coarse sand as a third choice, and that they reject substrate material bigger than 2 mm. The sand shrimp also prefer to burrow in substrates of brown colour, gold-sandy, grey-green and beige-sandy colour and reject white colour.

All the substrates used in these experiments, burnt to 600°C for 24 hours, were devoid of any organic matter, so food did not influence the results of the experiments. Although the shrimp were not fed during the experiments, from 120 shrimp examined after all the replicates, 2 had full stomach, 12 half full, 39 small amount and 67 had empty stomachs.

Price (1962) and Wilcox (1972) found sand in the gastric mills of the sand shrimp. Stomachs were not opened, but there is no doubt that the shrimp consume the substrate, maybe deriving some benefits from bacteria and, perhaps, algae and microflora which grow on the substrate and on which shrimp browse, as Wilcox and Jeffries (1974) report. Meadows (1964) reports that films of micro-organisms develop quickly on the surface of objects newly immersed in water, reaching the number 1.24×10^7 bacteria/cm^2 (according to ZoBell, 1946). Forster (1953) has shown that it is nearly impossible to starve caridean shrimp in captivity, because they will eat

their own feces which contain cultures of ciliates. The same was also demonstrated by Frankenberg and Smith (1967) for crustaceans, polychaetes, gastropods. pelecypods and teleosts. Thus, the shrimp may eat their own feces and they may have consumed parts of cast exoskeletons as well. These are the obvious reasons for the stomach contents of the shrimp in the experiment, sand being the more visible.

Wilcox (1972) reports that appendages and mouth-parts of the shrimp are modified for collecting and ingesting small particles, such as benthic diatoms. Although it needs further investigation, the abrupt decrease of selectivity in substrates with particle sizes bigger than 2 mm may be due to the fact that the sand shrimp cannot consume such particles. On the other hand, small particles should be easily consumed, and this could explain the smooth falling of selectivity with decrease in particle size.

Aside from the food supply, Williams (1955a) emphasized the importance of cover in nursery areas. It would appear that the need to find cover may be complemenary to a need of food. Cover may take the form of vegetation, debris-strewn bottom, or the substrate itself (Williams, 1958). Verwey (1948) emphasises that burrowing forms seek shelter under the sand. Thus the substrate, aside from the food, appears to exert an influence on the shrimp.

Wieser (1959) found that, for mechanical reasons, fine sand is more favorable than coarse to some invertebrates.

This capacity to burrow may provide another reason why the sand shrimp avoids substrates with particle size bigger than 2 mm. As was described, shoveling with the antennae completes the burrowing. If the grains are so big that the animal is not able to remove them with the antennae and put them on its back, this will result in a partially-covered shrimp. As an obvious result, the animal will avoid these particle sizes.

According to Williams (1958), the animals adjust burrowing not only to the ease with which they can enter the substrate, but also to their respiratory requirements. Observations on shrimps burrowed in silt and clay showed that their gill chambers were not clean because small particles of the substrate were attached to the gills. This may be the reason why the number of shrimp which prefer these substrates is smaller than the number which prefer the sand.

The sand shrimp not only possess an innate burrowing behaviour, but also the possibility for active colour change (Verwey, 1948). The shrimp is not only dark over a dark background and light over a light one, but is assumes an appropriate tint for a yellowish or more brownish background by movements of appropriate types of pigment (Parker 1930). This means that, when not on the move, the animal is not easily seen; the shrimp's camouflage affords an excellent hiding.

Fingerman and Fingerman (1971, 1972), using Bio-Gel

P6 and eyestalk extracts from *C. septemspinosa*, separated a black pigment-dispersing substance from one which caused pigment concentration in this shrimp; these substances are mutually antagonistic. Fingerman (1973) found that not only black chromatophores, but also the red and white chromatophores of *C. septemspinosa* are under dual control by pigment-dispersing and pigment-concentrating substances. The fractions obtained from a Bio-Gel P6 column revealed black, red and white pigment activities all having their maxima in the same fraction. Fingerman states that the genus *Crangon* stands alone among crustaceans with respect to its chromatic response following eyestalk removal, because in his experiments a fraction was obtained which caused black pigment concentration without causing concentration of the pigment in red and white chromatophores. He states that a substance with only one pigment - concentrating activity and another with three pigment-concentrating activities due to a single substance would provide the shrimp with a means of finely modulating its chromatophore responses to different coloured backrounds.

In this respect, the fact that shrimp have a choice of a certain colour of substrate should be seen in the ease with which they control the chromatophores and match their colour with that of the substrate. Preference to the brown colour may indicate that the shrimp control the white chromatophores easier. Avoidance of the white substrate may show some difficulty in controlling the red and black chromatophores in this colour.

C. Feeding Experiments

1. Increase in the Weight and the Length and Amino acid analysis.

From the results of the feeding experiments the diets used can be ranked in the following order: Mussel - Combinations of mussel - Squid - Squid and Fish combinations - Fish (caplin) - TetraMin - TetraMin and fish combinations - Starved. Mussel is the best diet. Even its combinations with TetraMin, the poorest diet, became better when mussel was added to the diet. Combinations like this are likely to form a nutritionally more complete diet by providing the necessary nutritive elements which the less effective diet lacks. Squid comes after the combinations with mussel, followed by its combinations with fish. Within the group, squid appears more effective than caplin. Fish is less effective, and TetraMin and its combinations with fish are the poorest diets.

Mussel is considered as one of the best diets for prawn and shrimp. Wilcox (1972) reports that *Crangon septemspinosa*, although feeding at night, will be stimulated and eat fresh mussel during the day. Reeve (1969), Forster (1970), Wickins (1972a), and Forster and Beard (1973), found the mussel to be the best food for *Palaemon serratus*, and Wickins (1972b), found it the most satisfactory food for juveniles and adults of the spot prawn *Pandalus platyceros* and the giant freshwater prawn *Macrobrachium rosenbergii*. Finally, in Japan the Kuruma-shrimp is occasionally fed with mussel which is considered as excellent feed (Shigueno 1975). From the results of the present experiments it is obvious that no

other food or combination of the ones used is better than mussel.

Feeding experiments with *Crangon septemspinosa* were also conducted by Wilcox (1972) and Wilcox and Jeffries (1974). Foods used were classified into four categories: Category I - Fresh or frozen animal tissues generally of marine origin (*Mercenaria*, *Artemia*, and hard-boiled egg). Category II - Dried animal tissues of marine origin (*Crangon*, fish meal, *Mercenaria*, Copepods and *Artemia*). Category III - Dried animal and microbial tissues (beef liver, marine yeast, agar, TetraMin, Bakers yeast, *Spartina* detritus, bacteria). Category IV - Starved. Within each category most treatments were found to produce equal growth rates. The shrimp grew best when eating fresh animal tissues, generally of marine origin, which are the preferred foods in nature, but to lesser extent they grew on other organic material.

Discussing their results, they suggested that olfactory quality could account for the different rates of growth between the various categories, because drying removed enough of the chemical stimuli and reduced the olfactory quality. Comparing the growths in the Categories, they say that the foods of non-marine origin could be lacking the olfactory chemicals that evoke feeding responses or could be low in essential amino acids, lipids or other nutrients required by the shrimp. In contrast, when hard-boiled egg was fed to the shrimp, growth was equal with shrimp fed foods of marine origin. The chemical stimulus for feeding appeared to be

general, because non-marine foods evoked the response, but foods preserved by drying were not ingested. Heat or freezing, they suggest, modify or remove water soluble compounds that are responsible for initiating the feeding response. "The unsuitability of dried foods, then, is not necessarily in the nutritional quality of the food, but in the ability of the shrimp to locate it." The same authors (1974, 1976) totally attributed the difference in growth performance between the fresh and dried diets to the olfactory quality.

Wilcox and Jeffries conducted their experiments putting 3 sand shrimp of each size class in containers 20x20x40 cm. It is difficult to explain how 3 active *Crangon* were not able to locate any kind of food in these containers, when the same authors conclude that "if hungry it will ingest a variety of substances until satisfied," and especially when they observed that the sand shrimp even ingest, the substratum. Their explanation may be true; olfactory differences as stimuli may exist. However, in cases where the food can be easily found, the unsuitability of the foods should be searched not in the stimuli to find it and ingest it, but in the nutritional value of the food, i.e. the proteins, amino acids, lipids etc. It is known that heating and drying of the food oxidizes some amino acids (tryptophan and cystein). The unsuitability of dried foods then is probably in the nutritional quality of the food.

Because foods were often non ingested, does not mean that they are hot suitable. Shigueno (1975) describes

studies at the Kagoshima Perfecture Fisheries Research Station and notes: "The maximum consumption of food with high content of palatable items did not necessarily produce faster growth... As to the quantity of food, it was observed that food lacking in nutritive elements was eaten more, while food containing the same nutrients in proper amounts, though eaten less, brought fast growth." There is no doubt that the olfactory quality of a diet evokes feeding responses, so it will be eaten more. These diets happen to be the ones giving better growth, but this does not mean that these diets are always the most effective ones.

Although Wilcox and Jeffries speak about the lack of chemicals to evoke feeding responses in the dried foods and in the foods of non marine origin, they classify hard-boiled egg in the category of foods of marine origin. It is not easily understood, then, how the egg evoked chemical stimuli similar to those foods.

It would have been expected that combined diets give better results than the single food diets. However, the results of the present experiments have indicated that mussel as a single diet gives better results than all the other diets fed singly or in combination. From the ranking of the diets it has been shown that the other single diets give better growth than some combined ones. The findings on this point vary: -

Forster (1970) fed newly-metamorphosed juvenile prawn *Palaemon serratus* with the following foods: Female

crab gonad and digestive gland, shrimp, lugworm, mussel gonad and combinations of two of the above, i.e. crab + lugworm, crab + mussel, shrimp + mussel, lugworm + mussel, etc. His results showed that there was no significantly improved survival or growth on any of the single food diets or any of the combined diets. However, there was a highly significant increase in growth on combined food diets when compared with single food. Also, there was no improved survival between juveniles fed on single and combined foods. Forster attributed the improved growth on combined food diets to the juveniles eating more when fed with two foods, or to the two foods forming a nutritionally more complete diet, giving more rapid growth.

When Forster fed later juveniles from about 2 weeks after metamorphosis with single and combined foods, no difference in growth was observed.

In Japan two lots of *Panaeus japonicus* were reared under two different feedings (Shigueno, 1975); one lot was fed only clam meat, and the other, both clam and squid which was frozen when fresh. The results of the experiment showed that the per cent gain was about 70% higher in the lot fed mixed diet than in the other fed a single diet. The better growth of shrimp given the mixed diet was attributed to the compensating nutritive elements possessed by squid meat but absent in clam.

In both cases the better growth is attributed to the compensating nutritive elements possessed by the one

food but absent from the other. The explanation of why combined diets in the experiments reported here did not give better results than mussel, may lie in the fact that mussel itself is such a complete diet that squid, caplin and TetraMin do not possess the compensating nutritive elements to form a better diet than the mussel alone. This might have happened in the above mentioned studies: crab, lugworm and shrimp may have possessed elements to complete mussel; squid may have supplemented the short-necked clam; but this may not happen with the diets in the present experiments.

Forster and Beard (1973) undertook growth experiments with the prawn *Palaemon serratus* fed with fresh and compounded foods; they showed that growth was influenced by a dietary protein level up to about 30 per cent protein, but above this level growth was influenced to a lesser extent. They suggested that optimum protein levels in the diets for that prawn were likely to lie between 30 and 40 per cent. These results, they said, were in general agreement with optimum protein levels found for some fish. It is known that the favourable content of crude protein in the fish feed ranges roughly from 40-60% depending on the species of the fish.

Deshimaru and Shigeno (1972), dealing with artificial diets for the prawn *Penaeus japonicus*, showed a close relation between the protein content in the diet and its feed-efficiency. They proved that a higher protein level is required for prawn than for fishes. As a standard scale to evaluate the nutritional value of feed protein, Phillips and Brockway (1956)

suggested that the feed having an essential amino acid composition similar to that of the objective animal would be the best. Deshimaru and Shigeno (1972) report that Ogino (1963) supports this suggestion. Further, Deshimaru and Shigeno made amino acid analyses on feeds which were graded in classes of feed efficiencies (below 60%, 60-80%, 80-90%, over 90%); they used diets which included fish and squid meal, short-necked clam and *P. japonicus*. Their results indicated that the feeds with efficiencies below 60% contained more compounds falling on the acidic side, such as aspartic acid, threonine, serine, glutamic acid, proline, glycine, etc., whereas the feeds with efficiencies over 60% showed higher contents of basic amino acids like lysine and histidine. Highly significant was the finding of the analyses that animo acid composition of the feeds with higher efficiency were approximately the same as those found in the shrimp. Furthermore, the composition of short-necked clam, and that of squid meal, were found to be very close to that of the shrimp. Fish meal was found to be quite different from shrimp, being short in the content of basic amino acids like phenylalanine, lysine, histidine and arginine. These four amino acids were also confirmed to be essential to the prawn *Palaemon serratus* by Cowey and Forster (1971), together with six more amino acids - threonine, valine, methonine, isoleucine, leucine, and trytophan. Shigueno (1975) believed that the same amino acids are essential for *Penaeus japonicus*, and Harrison (1976) concluded that the essential amino acid requirements anywhere in the animal kingdom probably have little deviation from a basic pattern.

The results of the amino acid analyses in this study show that the amino acid composition of the mussel is closest to that of the shrimp; the composition of the squid and caplin have less similarities with the composition of the shrimp, and the amino acid composition of TetraMin is very different than that of the shrimp.

These results fully agree with Deshimaru and Shigeno's discovery that the amino acid distribution ratios of the best diets have close similarity to that of the shrimp. It is now easily explained why mussel, combined with squid, caplin and TetraMin, foods with lower efficiency, gives diets with high efficiency. M+T, for example, is a highly effective diet, because the amino acids in mussel compensate the amino acids absent from TetraMin. On the other hand, C+T is not an effective diet, because caplin cannot compensate the amino acids absent from TetraMin. On the contrary, the acidic amino acids of the two foods, added together, produce a food with very high content in these amino acids, which result in a very inefficient diet.

The order of classification of the diets in this study and the order of the Japanese authors are similar. Wilcox (1972) and Wilcox and Jeffries (1974) classification of diets rather agrees with the classification according to the amino acid composition of the diet, although it has been proved that all animal tissues of marine origin cannot be included collectively in one category. If they had emphasized nutrition instead of olfaction, they might have

found the answer there.

2. Moulting and Moulting frequency

It is shown in the results that the shortest intermoult period appears in the Mussel group, which gives the best growth rate. The intermoult period for the Squid and Fish group is longer and overlaps with that of the TetraMin group; these two groups give smaller growth rates than the Mussel group. Finally, the intermoult period for the Starved group is extremely long and hypothetical, and the growth rate is the worst of all the groups.

Meixner (1966), studying the effect of food supply on moulting, growth and spawning of *Crangon crangon*, emphasizes the influence of food on the intermoult periods. If the amount of food was insufficient to cover the metabolic needs, a large increase in the moulting intervals took place. Meixner (1966, 1969) found that temperature of sea water and body size play an important role in the moulting rhythm. The influence of sex is evident too.

Excluding temperature which was constant, the findings of Meixner agree with the results of this experiment. It can be concluded that not only the amount of food, but the quality of food as well, influence the moulting intervals, as was found in this study. Differences between groups exist and may be attributed to the effectiveness of the diets, this being another indication of the correctness of the classification stated.

The influence of food quality was noticed by

Plankemann (1935, according to Forster, 1970), who suggested that mussel diet, which is rich in glycogen, may influence the moulting frequency of *Leander squilla (Palaemon elegans)* and *Crangon crangon*. Experiments with the crustaceans *Astacus astacus, Homarus gammarus, Panulirus japonicus, Cancer pagurus, Callinectes sapidus* and *Penaeus japonicus* (according to Kazanawa et. al., 1971 and Forster and Beard, 1973) have shown that these species are incapable of synthesizing cholesterol and that this or others sterols are therefore required in the diet. Kazanawa et. al. (1971) also suggested that the prawn, similar to insects, require dietary sterol for normal growth, because they are not capable of biosynthesizing cholesterol from acetate. They assumed that cholesterol may be a precusor of a vitamin D, steroid hormone, moulting hormone and brain hormone. They demonstrated the bioconversion of cholesterol to moulting hormone, and observed an increase of number of moults in prawn fed a diet supplemented with cholesterol. It is possible then, that diets lacking these substances may affect the moulting frequency and growth in general.

All moulting of *Crangon vulgaris*, according to Hagerman (1973) occurred at night. Lloyd and Yonge (1947) agree, saying that this happens because of the habits of the animals, which normally leave the protection of the substrate only in darkness. This generally agrees with what was observed in the laboratory, where the cast exoskeletons were found in the morning.

Hagerman (1973, 1976) points out that the moult is the most sensitive period of the life of a crustacean; mortality is often very high at this time. Excluding predation, mechanical difficulties arise in withdrawing from the old cuticle and physiological problems arise from difficulties in osmotic and ionic regulation. "If anything goes wrong, for instance if the moult is prolonged due to difficulties in casting the old cuticle or if the hardening of the new cuticle takes too long, *Crangon vulgaris* will rapidly die due to osmotic loss of important ions."

3. Growth rate

The overall classification of growth rates indicates a strong influence of the quality of food. This is in agreement with Meixner (1963) who states that growth rates are influenced by food, temperature and size.

Wilcox and Jeffries (1973) concluded that the growth rate of *Crangon septemspinosa* is a positive function of water temperature and a negative function of size. This is apparent in the present results. All size classes show the influence of food quality apart from the above factors.

Female *Crangon crangon* have a greater growth rate (Meixner 1968, 1969). This appears to be true for *C. septemspinosa*, except the IV size class of the TetraMin and Starved groups. These results suggest that female sand shrimp do not grow larger than the males in difficult and stressed conditions.

Wilcox (1972) indicated that the growth rate in

the laboratory were more than double than those of a field study at a comparable water temperature. The same conclusion can be reached from comparing the results of this study with the growth of the sand shrimp in Rhode Island (Wilcox and Jeffries 1973). Therefore it appears that the holding of the shrimp in the laboratory with an open seawater system is optimal and that factors such as water quality or food should be limiting. The variations in the growth rate are mainly attributed not to environmental parameters but to the controlled variable.

4. Survival

Survival of the shrimp is also related to the diets. The Mussel group, which showed the best growth, also has the best survival of the animals. The Starved group gave the worst growth and survival. The Squid and Fish group and the TetraMin group, giving intermediate growth, also have intermediate survival.

The deaths just before moulting may also give a similar conclusion. These deaths were also observed by Reeve (1969) and Forster (1970) when culturing the prawn *Palaemon serratus*. Reeve was able to pull off the rostrum and find the soft new rostrum beneath; he suggested that these deaths may have been caused because of dietary deficiencies. Although evidence was weak he attributed a major cause of mortality in stock prawns to the inadequacy of the diet. This fact, if combined (i) with the observation of apparently healthy animals which died before moulting

(ii) that this number of these deaths increased with the time of captivity, and (iii) with the results which show increasing numbers of deaths in less effective diets, indicates that Reeve's suggestion may be true. The superiority of mussel, for example and the inferiority of caplin and TetraMin in the survival do not have any other obvious cause than the adequancy of the diets. Since the experiment was made under optimum conditions of temperature and salinity (Haefner, 1969a), this suggests that the only other variable remaining was the food.

Survival of the starved shrimp was high. A female shrimp survived for about 13 weeks in starvation, while the bulk of the deaths appeared around the 7th week. The tolerance of the sand shrimp is very high. Forster (1953) reports that it is not at all easy to starve small carideans, because of their coprophagus habits. Frankenberg and Smith (1967) fed fecal pellets 20 marine species, including 7 crustaceans. They concluded that coprophagy plays a significant role in the trophic relationships of benthic communities. Since omnivory appears to be the predominant feeding habit among benthic organisms, they might obtain sufficient energy to meet a substantial portion of their metabolic needs. Further, it was mentioned that *C. septemspinosa* consume the substratum and browse on microorganisms which grow on it (Wilcox and Jeffries,1974). The fact that the starved animals were able to survive for so long, may suggest that they exhausted all their metabolic reserves,

and all the ways to obtain energy. The greater survival of the female shrimp over the male, may indicate that they have greater metabolic reserves.

VI. SUMMARY AND CONCLUSIONS

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The *Crangon septemspinosa* population in Long Pond has egg-carrying females from April to August. Juveniles appear throughout the year. The juvenile stages in August increase in size during the summer and fall and have no apparent increase during the winter. These shrimp mature by May and continue increasing in size by next summer and fall. Most of them disappear from the population and the remaining, already larger, shrimp migrate offshore with the cooling of the water, and then, inshore with the increase of temperature.

This pattern of migration is also supported by the appearance of egg-carrying females in the population and the egg stages carried by them. It is suggested that these animals migrate offshore in September and inshore in April.

The fact that juveniles have their main peak in August and that they were collected in almost all the collections, indicates a single but extended breeding season. The appearance of the juveniles in the population inshore in April, is then due to recruitment from this extended breeding season.

Female shrimp live for about three years and grow larger than the males, which live more than two years.

Crangon septemspinosa develop their external sexual characteristics in Newfoundland at shorter lengths than their southern counterparts.

When, burrowing, the sand shrimp excavates a hole using the pleopods and then forces itself in it,

sinking horizontally in the substrate. Then it moves and flattens the substrate over its back with the antennae which, at the end of the action, rest backwards along the animal's body.

All of the burrow observations made in this and other studies show that the shrimp penetrate the bottom so that their dorsal surfaces are just below the surface of the substrate. The depth of burrowing is related to the animal's preference as regards to the hardness of the substrate; the sand shrimp, specializing in soft substrates, do not burrow deep in it, contrary to species burrowing in hard substrates which tend to bury themselves more deeply.

Crangon septemspinosa prefer sand (0.250-0.500mm) to burrow in. The sand shrimp may be able to choose among clay, silt and all kinds of sand, but it does not choose to burrow in granules or pebble. The reason is probably because it cannot burrow in these particle sizes, either because of mechanical reasons - use of the antennae to cover itself - or because of physiological reasons - modification of the mouthparts to ingest the sand and utilize it for food trituration and for nutritional benefits.

The sand shrimp chose to burrow in brown substrates as their first preference, followed by gold-sandy, grey green, beige sandy and white-grey colours. The colour of the preferred substrate may influence the distribution in a certain bottom type. Since none of the colours used in this study was fully rejected, this influence is probably small.

The laboratory experiments have shown that under controlled temperature conditions the growth of *Crangon septemspinosa* fed single and combined foods of marine origin is not the same in all the diets. Differences in the increase of the weight, the lengths and the moulting frequencies of the animals, as well as their survival, permit the classification of the diets into four groups: α' Mussel group; β' Squid and Fish group γ' TetraMin group; δ' Starved group. Within each group the calculated growth show no significant differences.

The reason for these differences may lie in the amount of crude protein content of the diets and especially the proportions of the amino acids. The efficiency of the diets supports the findings of Phillips and Brockway (1956) and Ogino (1963) that the food having an essential amino acid composition similar to that of the effective animal is the best. The amino acid analyses of the feeds made show that effective diets, such as the diets of the Mussel group, have similar amino acid proportions to that of the shrimp; non effective diets, such as the ones in the TetraMin group, differ from the shrimp in the amino acid distribution.

In this respect, foods that are preserved by drying are less satisfactory because heat or dry-freeze modify their nutritive value. If any food substance does not meet the criteria of the amino acid distribution, even if it evokes feeding responses, will not result in a better growth. Poor growth observed in several diets probably are due to nutritional deficiencies of the diets.

A definite relationship was also found between growth in the diet groups and the moulting frequency, as well as the growth rate: The diets in the Mussel group gave the best increments in the length and the weight; the intermoult period in this group is the shortest of all the groups, while the growth rate of the group is the biggest. The Squid and Fish group, including less efficient diets have longer intermoult periods; these overlap with the diets of the TetraMin group which includes even less efficient diets. The growth rates in these two groups are smaller than the first one. The intermoult period of the Starved group is the greatest of all, and its growth rate, the worst.

Survival was also correlated with the groups of diets in the order stated. Better diets give higher survival. The deaths just before the expected moulting in inadequate diets is a further evidence on this point.

Survival, moulting frequency, increase in length and weight and overall growth rate agree in the ranking of the diets, with mussel giving the best results.

The superiority of mussel mantle and mussel-combined diets suggest that they meet all the requirement which stimulate growth in the sand shrimp. A major disadvantage of mussel as a standart food is that the condition and probably therefore the food value of its mantle varies seasonally in relation to the breeding cycle. However, growth with mussel itself was superior to all the combined diets for a period of 224 days in this study. This indicates its suitability as a diet for *Crangon septemspinosa*.

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APPENDIX 1

CONTROL: TEST OF DISTRIBUTION

a) Shrimp put in such a way to make sure that two shrimp were burrowed in each division at the beginning of the experiment. Coarse sand in all divisions.

Date	Temp. °C	DIVISIONS									
		1	2	3	4	5	6	7	8	9	10
April 19	3.0	2	2	3	-	2	1	2	4	3	1
April 20	2.5	3	2	3	3	-	-	3	3	2	1
April 21	2.5	4	3	3	1	1	1	3	-	3	1
April 22	2.5	-	1	3	1	2	2	1	3	4	3
April 23	3.0	2	2	1	4	2	2	2	2	2	1
TOTAL		11	10	13	9	7	6	11	12	14	7

b) Shrimp released in the middle of the tank at the beginning of the experiment. Coarse sand in all the divisions.

Date	Temp. °C	DIVISIONS									
		1	2	3	4	5	6	7	8	9	10
April 24	2.0	-	2	1	2	-	2	2	5	1	5
April 25	2.0	3	2	1	2	1	-	3	2	3	3
April 26	2.0	6	1	3	1	2	-	1	-	2	4
April 27	2.0	1	1	4	3	2	3	1	1	1	3
April 28	2.0	2	3	1	2	3	2	2	-	4	1
April 29	2.5	3	1	4	3	2	3	1	1	2	-
April 30	2.5	5	1	2	1	-	1	2	5	1	2
TOTAL		20	11	16	14	10	11	12	14	14	18

APPENDIX 2

Experiment 1: Particle size choice - 1st replication: Results

Date	Temp. °C	DIVISIONS									
		1	2	3	4	5	6	7	8	9	10
		1-2mm	0.250-0.500mm	4mm	0.020 0.063mm	0.5-1mm	0.063-0.100mm	3-4mm	0.100-0.250mm	2-3mm	0.002-0.020mm
		Very Coarse Sand	Sand	Pebble	Silt	Coarse Sand	Very Fine Sand	Coarse Granule	Fine Sand	Find Granule	Clay
May 16	4	-	4	-	4	3	4	-	5	-	-
May 17	5	1	6	-	3	1	2	-	4	-	3
May 18	6	-	4	-	6	2	3	-	4	-	1
May 19	5.5	1	4	-	2	2	2	-	6	-	3
May 20	6	2	7	-	1	2	2	-	4	-	2
May 21	6	2	4	-	1	2	4	-	6	-	1
May 22	5	1	9	-	3	-	3	-	2	-	2
May 23	4	1	7	-	2	2	3	-	4	-	1
May 24	4.5	1	8	-	1	5	3	-	1	-	1
May 25	4	2	7	-	1	3	3	-	4	-	-
TOTAL		11	60	-	24	22	29	-	40	-	14

Number of shrimp: 20, i.e. 10 males and 10 females

Carapace length: 7 mm

Total length: 40-43 mm

Tank covered to avoid possible orientation

STOMACH FULLNESS

0 - Empty	10
1 - Small amount	9
2 - Half full	1
3 - Full	-
4 - Distended	-

APPENDIX 3

Experiment 1: Particule size choice - 2nd replication: Results

Date	Temp. °C	DIVISIONS									
		1	2	3	4	5	6	7	8	9	10
		1-2mm	0.250-0.500mm	4mm	0.020 0.063mm	0.5-1mm	0.063-0.100mm	3-4mm	0.100-0.250mm	2-3mm	0.002-0.020
		Very Coarse Sand	Sand	Pebble	Silt	Coarse Sand	Very Fine Sand	Coarse Granule	Fine Sand	Fine Granule	Clay
June 15	8.0	1	7	-	1	2	2	-	4	-	3
June 16	7.0	1	5	-	1	3	5	-	4	-	1
June 17	7.0	1	6	-	1	4	4	-	3	-	1
June 18	7.0	-	6	-	3	6	3	-	2	-	-
June 19	4.0	2	4	-	2	3	2	-	5	-	2
June 20	3.0	1	5	-	3	3	3	-	4	-	1
June 21	9.0	1	8	-	1	2	3	-	3	-	2
June 22	9.0	2	5	-	1	2	3	-	5	-	2
June 23	7.5	2	6	-	2	1	4	-	4	-	1
June 24	8.0	1	7	-	2	3	3	-	4	-	-
TOTAL		12	59	-	17	29	32	-	38	-	13

Number of shrimp: 20 ie. 10 males and 10 females

Carapace length : 7 mm.

Total length: 40-43 mm.

Tank covered

STOMACH FULLNESS

0 - Empty	11
1 - Small amount	6
2 - Half full	3
3 - Full	-
4 - Distended	-

APPENDIX 4

Experiment 1: Particle size choice - 3rd replication: Results

Date	Temp. °C	DIVISIONS 1	2	3	4	5	6	7	8	9	10
		1-2mm	0.250-0.500mm	4mm	0.020 0.063mm	0.5-1mm	0.063-0.100mm	3-4mm	0.100-0.250mm	2-3mm	0.002-0.020mm
		Very Coarse Sand	Sand	Pebble	Silt	Coarse Sand	Very Fine Sand	Coarse Granule	Fine Sand	Fine Granule	Clay
June 28	15.0	1	4	-	2	5	3	-	4	-	1
June 29	10.0	2	6	-	1	4	3	-	3	-	1
June 30	13.0	1	4	-	1	3	5	-	5	-	1
July 1	10.5	1	7	-	2	4	2	-	4	-	-
July 2	12.0	2	6	-	2	2	3	-	4	-	1
July 3	14.0	-	6	-	1	2	3	-	4	-	4
July 4	14.5	1	5	-	3	3	4	-	3	-	1
July 5	12.0	-	5	-	1	4	3	-	5	-	2
July 6	16.5	1	5	-	2	4	3	-	4	-	1
July 7	12.0	1	5	-	2	2	4	-	4	-	2
TOTAL		10	53	-	17	33	33	-	40	-	14

Number of shrimp: 20 - ie. 10 males and 10 females

Carapace length: 7 mm

Total length: 40-43 mm

Tank covered

STOMACH FULLNESS

0 - Empty	10
1 - Small amount	5
2 - Half full	3
3 - Full	2
4 - Distended	-

APPENDIX 5

Experiment 2 - Colour Choice - 1st replication: Results

Date	Temp. °C	DIVISIONS					
		1	3	5	7	9	Out
		White-Grey	Pink-Sandy	Beige-Sandy	Brown	Grey-Green	
Oct. 20	10.0	2	5	2	4	4	3
Oct. 21	11.0	2	4	5	5	2	2
Oct. 22	10.0	1	6	3	5	3	2
Oct. 23	11.0	2	4	4	5	5	-
Oct. 24	10.0	1	5	4	4	3	3
Oct. 25	10.0	2	3	4	5	5	1
Oct. 26	9.0	3	3	2	5	4	3
Oct. 27	9.2	2	5	3	5	5	-
Oct. 28	8.0	1	4	4	6	5	-
Oct. 29	8.7	-	5	4	4	7	-
TOTAL		16	44	35	48	43	14

Number of shrimp: 20, i.e. 10 ♂ and 10 ♀
Carapace length : 7-8 mm
Total length: 40-45 mm
Tank not covered
Sand (250-500 µ) in all divisions
There is no sand in the divisions 2,4,6,8,and 10
Shrimp starved.

STOMACH FULLNESS

0 - Empty	14
1 - Small amount	5
2 - Half full	1
3 - Full (not distended)	-
4 - Distended	-

APPENDIX 6

Experiment 2 - Colour choice - 2nd replication: Results

Date	Temp. °C	DIVISIONS					
		1	3	5	7	9	Out
		White-Grey	Pink-Sandy	Beige-Sandy	Brown	Grey-Green	
Oct. 30	10.0	2	5	2	4	6	1
Oct. 31	9.0	1	6	4	5	3	1
Nov. 1	9.0	-	9	3	3	4	1
Nov. 2	8.5	1	5	2	7	3	2
Nov. 3	9.0	2	3	3	4	5	3
Nov. 4	8.5	2	3	3	6	5	1
Nov. 5	9.0	3	4	4	5	3	1
Nov. 6	8.5	4	3	3	6	3	1
Nov. 7	9.0	3	4	3	7	2	1
Nov. 8	7.8	2	2	3	4	2	7
TOTAL		20	44	30	51	36	19

Number of shrimp: 20, i.e. 10 ♂ and 10 ♀
Carapace length: 7-8 mm
Total length: 40-45 mm
Tank not covered.
Sand (250-500 μ) in all divisions
No sand in the divisions 2,3,6,8 and 10
New position of the tank

STOMACH FULLNESS

0 - Empty	12
1 - Small amount	6
2 - Half full	2
3 - Full (not distended)	-
4 - Distended	-

APPENDIX 7

Experiment 2 - Colour Choice - 3rd replication: Results

Date	Temp. °C	DIVISIONS					
		1	3	5	7	9	Out
		White-Grey	Pink-Sandy	Beige-Sandy	Brown	Grey-Green	
Nov. 9	6.5	1	3	2	9	3	2
Nov. 10	7.0	2	5	4	6	3	-
Nov. 11	7.0	2	5	3	4	3	3
Nov. 12	7.5	2	2	4	4	4	4
Nov. 13	8.0	1	3	6	4	4	2
Nov. 14	6.0	2	7	4	2	5	-
Nov. 15	6.0	2	3	3	6	4	2
Nov. 16	5.0	2	3	3	5	4	3
Nov. 17	4.5	1	6	3	4	3	3
Nov. 18	4.0	2	5	3	5	3	2
TOTAL		17	42	35	49	36	21

Number of shrimp: 20, i.e. 10 ♂ and 10 ♀

Carapace length : 7-8 mm

Total length: 40-45mm

Tank not covered.

Sand (250-500 µ) in all divisions

No sand in the divisions 2,4,6,8 and 10

Shrimp starved

New position of the tank

STOMACH FULLNESS

0 - Empty	10
1 - Small amount	8
2 - Half full	2
3 - Full (not distended)	-
4 - Distended	-

APPENDIX 8

Similarities and Differences of the Weight in the diets of the first feeding experiment.

S+M+C	S+M	S+M+T	M+T	M+C+T	S+M+C+T	M+C	Squid	S+C	S+T	Caplin	S+C+T	Tetramin	C+T	Starved	DIETS
S	S	S	S	S	S	D	D	D	D	D	D	D	D	D	Mussel
	S	S	S	S	S	D	D	D	D	D	D	D	D	D	S+M+C
		S	S	S	S	S	D	D	D	D	D	D	D	D	S+M
			S	S	S	S	D	D	D	D	D	D	D	D	S+M+T
				S	S	S	D	D	D	D	D	D	D	D	M+T
					S	S	D	D	D	D	D	D	D	D	M+C+T
						S	D	D	D	D	D	D	D	D	S+M+C+T
							S	D	D	D	D	D	D	D	M+C
								S	S	S	S	D	D	D	Squid
									S	S	S	S	D	D	S+C
										S	S	S	D	D	S+T
											S	S	S	D	Caplin
												S	S	D	S+C+T
													S	D	Tetramin
														D	C+T

S = Similar diets

D = Significantly different $P < 0.05$

APPENDIX 9

Similarities and Differences of the Length in the diets of the first feeding experiment.

S+M	S+M+C	S+M+T	M+T	M+C+T	S+M+C+T	M+C	Squid	S+C	S+T	S+C+T	Caplin	Tetramin	C+T	Starved	DIETS
S	S	S	S	S	D	D	D	D	D	D	D	D	D	D	Mussel
	S	S	S	S	S	S	D	D	D	D	D	D	D	D	S+M
		S	S	S	S	S	D	D	D	D	D	D	D	D	S+M+C
			S	S	S	S	D	D	D	D	D	D	D	D	S+M+T
				S	S	S	D	D	D	D	D	D	D	D	M+T
					S	S	D	D	D	D	D	D	D	D	M+C+T
						S	D	D	D	D	D	D	D	D	S+M+C+T
							D	D	D	D	D	D	D	D	M+C
								S	S	S	S	D	D	D	Squid
									S	S	S	D	D	D	S+C
										S	S	S	D	D	S+T
											S	S	D	D	S+C+T
												S	S	D	Caplin
													S	S	Tetramin
														S	C+T

S = Similar diets

D = Significantly different $P < 0.05$

APPENDIX 10

Growth rate per week in mm for the diets and the groups

	DIETS	III Size Class				IV Size Class				III and IV Size Classes	
		MALE	N	FEMALE	N	♂ + ♀ for the classes	N	MALE	N	FEMALE	N	♂ + ♀ for the classes	N	Average of the classes	N
Mussel Group	Mussel 1	1.7872341	6	1.4640522	10	1.5852453	16	0.8060606	16	1.4072164	11	1.0509756	27	1.2497737	43
	Mussel 2	2.6611569	11	1.6554053	9	2.2085686	20	0.9136547	22	1.3611111	16	1.1020573	38	1.4836129	58
	S+M+T	1.5489361	14	1.666666	3	1.5697119	17	0.9079497	13	0.9444443	7	0.9207228	20	1.2189069	37
	S+M	1.0547945	12	1.8958333	3	1.2230022	15	0.9514563	11	1.050000	2	0.9666168	13	1.1039661	31
	S+M+C 1	1.0956522	6	1.750000	5	1.393083	11	0.5924764	16	2.10000	4	0.8939811	20	1.0710817	48
	S+M+C 2	1.1170212	11	1.6709677	9	1.3662971	20	0.8301886	17	0.711382	11	0.7535145	28	1.0262708	28
	S+M+C+T	1.1838235	16	0.9390243	5	1.1155379	21	0.7074468	10	0.995098	9	0.8437026	19	0.9916661	40
	M+C+T	1.0652173	8	0.777777	5	0.9546635	13	1.0689655	11	0.5505617	4	0.9307244	15	0.9418389	28
	M+C	0.7894736	13	1.6030534	8	1.0394087	21	0.7368421	9	0.6470588	5	0.7047766	14	0.9415557	35
	M+T	0.7233333	16	2.1724137	2	0.8843421	18	0.7692307	14	1.1666666	11	0.9441022	25	0.9190853	43
	Average for the Mussell Group	1.2610555	113	1.5215023	59	1.3504062	172	0.8280104	139	1.1177527	80	0.9338522	219	1.1170933	391
Squid and Fish Group	Squid 1	0.942857	14	0.8092485	10	0.8871867	24	0.5507614	19	0.9871794	4	0.6266601	23	0.7596949	47
	Squid 2	1.20000	12	0.910000	5	1.1147058	17	0.2664359	12	0.7807713	11	0.5124223	23	0.7683927	40
	S+C	0.7179487	6	1.1226415	6	0.920295	12	0.3987341	7	0.7403846	4	0.5229706	11	0.7302702	23
	S+C+T	0.5875918	14	1.000000	2	0.6191428	16	0.26*2307	1	1.0208333	2	0.7702991	3	0.6598516	19
	S+T	0.715555	12	0.4117647	1	0.6547973	15	0.4516129	12	0.7403846	5	0.5365457	17	0.5919761	32
	Caplin 1	0.691358	4	0.4516129	1	0.6434089	5	0.3081761	7	0.4941177	3	0.3639585	10	0.4571263	15
	Caplin 2	0.5915492	7	0.5526315	2	0.5829008	9	0.339207	9	0.2832369	6	0.3168189	15	0.4165995	24
	Average for the Squid+Fish Group	0.8066703	69	0.8334656	29	0.8142593	98	0.4082315	67	0.6978314	35	0.5075738	102	0.6578496	200
Tetramin Group	Tetramin	0.5051546	9	0.530303	6	0.5152139	15	0.4262426	3	0.2658227	3	0.3450325	6	0.4665906	21
	C+T	0.4958333	12	0.4827586	3	0.4932183	15	0.2413793	4	0.3043478	1	0.253973	5	0.4334069	20
	Average for the Tetramin Group	0.4998281	21	0.5144548	9	0.5042161	30	0.3197492	7	0.2754549	4	0.3038418	11	0.4504034	41
Starved Group	Starved 1	0.2613793	2			0.2613793	2							0.2613793	2
	Starved 2	0.29166666	2			0.29166666	2			0.122807	4	0.122807	4	0.1790935	6
	Average for the Starved Group	0.2665231	4			0.2665231	4			0.122807	4	0.122807	4	0.194665	8

Calculations as in Table 14.

N = number of observations

APPENDIX 11

Days of Survival of *Crangon septemspinosa* in the diets of the first and the long-term feeding experiments

Mussel	S+M+C	S+M	S+M+T	M+T	M+C+T	S+M+C+T	M+C
29	69*	18	44*	77*	71*	45	37*
29	71	53	48	94	73	50	71
86	71	59	71	97	77	72	72
86	71	59	80	A	79	73	72
92	73	60	86	A	80	85	74
94	74	85	95	A	82	86	78
102	75	86	A	A	89	95	79
107	85	94	A	A	90	101	91
(199)	94	102	A	A	99	105	A
(221)	(169)	103*	A	A	A	A	A
(A)	(182)	A	A	A	A	A	A
(A)	(A)	A	A	A	A	A	A

Squid	S+C	S+T	Caplin	S+C+T	Tetramin	C+T	Starved
85	15	18	35*	26*	30	42	35
91	26*	23*	43	30	48	59	36
99	36*	54	48	35*	50*	64	38
99	67	59	50	41*	60	68	39
100	72	67	60	69*	67*	72	43
101	75	85	79	71	63	72	44
105	76	85	85	72	72	74	44
108	80*	86	89	74	72	79*	47
(124)	92	95	95	77	75	85	57
(135)	95	A	112	86	89	86	64
(142)	A	A	(119)	94	92	87*	79
(196)	A	A	(141)	A	99	90	89

* Shrimp which died due to moult failure

A Shrimp alive at the end of the experiment.
Brackets indicate survival of the long-term experiment.

APPENDIX 12

Days of survival of *Crangon septemspinosa* in the diets of the second feeding experiment

Mussel	S+M+C	Squid	Caplin	Starved
59	30	22	23*	26
88	38	24*	23	30
A	39*	31	25	30
A	48*	31	27*	32
A	49	33	30	36
A	49	33	31*	36
A	58	38*	31	43
A	63	40	32	44
A	65	63*	35	45
A	68	63	36	45
A	75	64	36	47
A	80	67	43	47
A	81	75	45	49
A	86*	80	58	55
A	95	80	58	55
A	A	81	61	57
A	A	82	65	57
A	A	94	80	59
A	A	94	86	59
A	A	95	88*	61
A	A	107	93	64
A	A	112	97	68
A	A	A	104	75
A	A	A	A	85

* Shrimp which died due to moult failure

A Shrimp alive at the end of the experiment